BOTANY
PRINCIPLES AND PROBLEMS

BY
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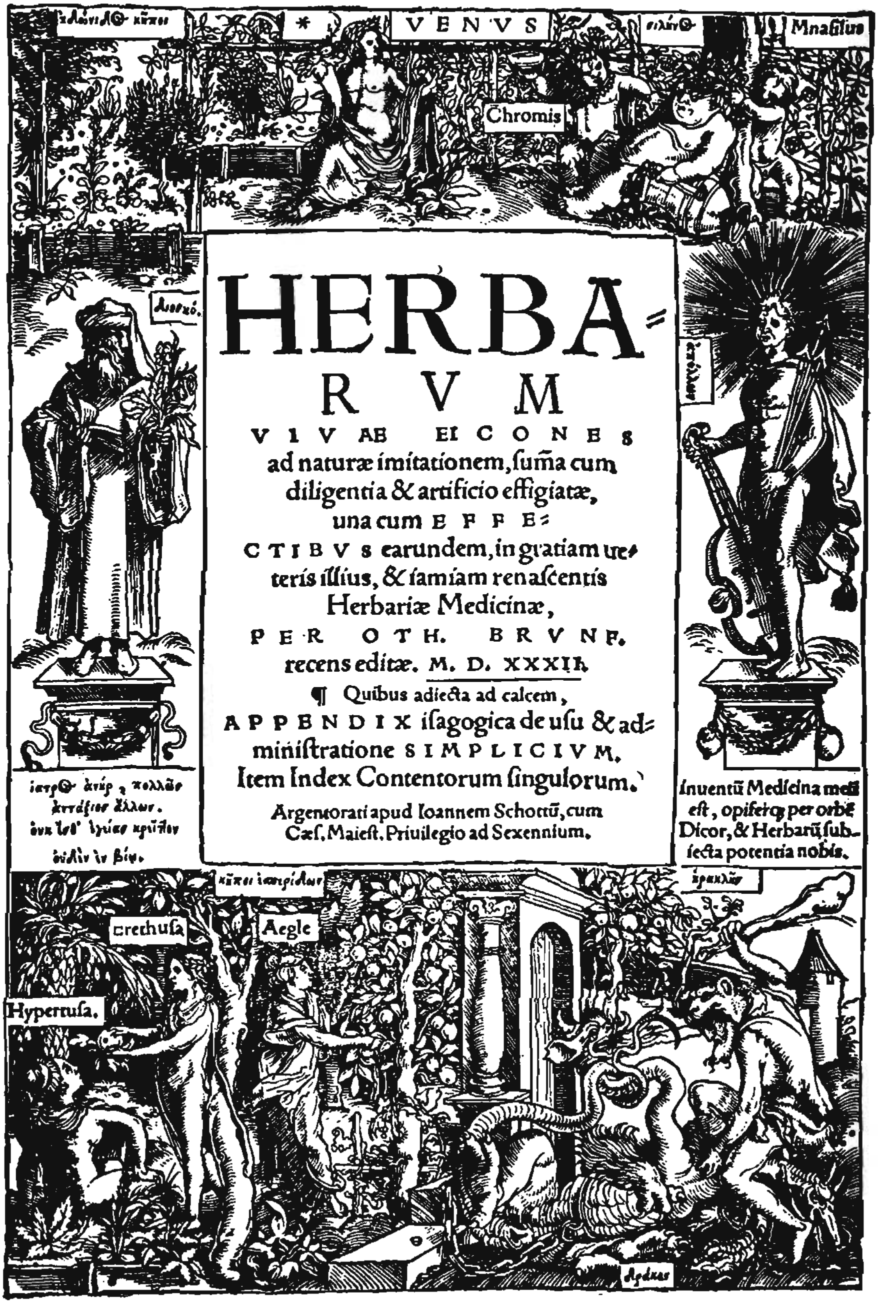

Frontispiece.—Title-page to an "Herbal" written by Otto Brunfels, and published in 1532.

PREFACE TO THE SECOND EDITION

In preparing the revision of this book the author has profited from the results of his own experience in using it as a text in elementary college botany in two institutions and from criticisms and suggestions offered by many other teachers. In its essential features the book is unaltered but there have been several rearrangements of material and changes of emphasis which, it is hoped, will prove of value. The material on the cell has been considerably increased and is now set apart as a separate chapter. The discussion of the soil and its relation to plant growth has been included under the chapter on the root. That portion of the chapter on the plant kingdom which dealt with the main steps in plant evolution has been incorporated in the chapter on plant evolution; and the portion on classification and nomenclature has been added to the chapter on the seed plants. The treatment of the thallophytes has been rearranged at a number of points. The text as a whole has been entirely rewritten and a considerable amount of additional material presented. Over thirty new illustrations have been added.

The Questions for Thought and Discussion, which are perhaps the most distinctive feature of the book and which have been successfully used by many teachers as the basis for class discussion, have been revised and their number slightly reduced. The Reference Problems have been considerably increased and somewhat broadened in scope.

The author is especially indebted to his colleague Dr. Tracy E. Hazen for helpful advice, particularly with reference to the chapter on the thallophyta. He is under obligation to Dr. R. A. Harper for the loan of an original copy of Brunfels' "Herbal," and to the authorities of the New York Botanical Garden for the use of three photographs from their collection. For permission to use illustrations from their published works, credit for which is duly given in the text in each instance, he is indebted to Dr. F. C. Bradford, Dr. A. H. R. Buller, Dr. C. W. Dodge, Dr. A. J. Eames, Dr. A. W. Haupt, Dr. T. E. Hazen, Dr. F. D. Heald, Dr. H. A. Jones, Dr. W. J. Morse, Dr. F. Ramaley, Dr. D. B.

Swingle, Dr. J. E. Weaver, and Dr. G. R. Wieland. To the many teachers and readers who have offered criticisms of the book and suggestions for its improvement, the author desires to express his very sincere thanks.

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May, 1929.

PREFACE TO THE FIRST EDITION

The present volume, an outgrowth of experience in presenting to college freshmen a course in elementary botany, endeavors to set forth somewhat briefly and concisely the more important facts concerning the morphology, physiology and classification of plants, and to provide a body of problem material which may be of assistance in stimulating thought and in promoting class discussion.

The consideration of structure and function in the earlier portions of the book is confined mainly to the seed plants, and the distinctive characteristics of the other members of the plant kingdom are discussed in the last five chapters. Should the course be too brief to take up these groups in detail, Chapter XIII, which deals with the main events in the history of the plant kingdom and the important features of its various divisions, may perhaps be used to give the student an idea of the kingdom as a whole. In view of the importance of the soil in the life of plants, and in order to emphasize the fact that living things cannot be understood without a knowledge of their environment, an early chapter is devoted entirely to the soil itself. The increased interest in matters pertaining to inheritance has warranted a special chapter on heredity and variation; and a chapter is also devoted to organic evolution, emphasizing its botanical aspects. The chapters have been so written as to be separately understandable and may readily be taken up in some other order than that in which they are here presented. The text is not primarily designed for agricultural students but many of the questions naturally involve a practical application of botanical principles and will perhaps commend themselves especially to those whose interest in botany is chiefly agricultural.

The rather extensive lists of "Questions for Thought and Discussion," which are perhaps the most novel feature of the present volume, have resulted from an attempt to stimulate within the student an attitude of interest, of curiosity and of critical thought toward the multitude of problems which plants present, and thus to provide him with a clearer insight into the way in which plants are constructed and function, and a firmer

command of botanical science in general, than can be given him merely through a series of lectures and recitations. Anyone who has mastered the facts presented in the text and who has at his command a reasonably broad body of experience, ought to be able, through the exercise of a little thought, to prepare satisfactory answers for all of them. "Thought questions" are by no means new in botanical pedagogy, but it is believed that no previous text has employed them to quite such an extent as does the present one. It is hoped that their inclusion here may encourage a method of class-room procedure more satisfactory than the common but somewhat outworn practice wherein a monopoly of thinking and talking is enjoyed by the instructor, and the student is chiefly required to memorize a series of what often seem to him to be unrelated facts. The "Reference Problems" are designed to send the student occasionally to other sources of information than his textbook, and thus to broaden his point of view and dispel from his mind the comfortable assurance that any particular authority may be infallible.

To all those who have been of assistance in the preparation of the book the author desires to express his sincere thanks. Many of his colleagues have contributed helpful suggestions and information in matters relating to their special fields, and to Professor G. S. Torrey is he especially indebted for advice and assistance during the course of the work. Professor Torrey and Dr. L. C. Dunn have been good enough to read and criticize portions of the manuscript. A. I. Weinstein has been helpful in many ways. Professor M. L. Fernald of the Gray Herbarium kindly supplied the data used in Figs. 131, 132 and 133. To Professor B. M. Davis of the University of Michigan and Professor J. W. Harshberger of the University of Pennsylvania the author is under obligation for their courtesy in providing material and facilities for the preparation of a number of the figures. He is also much indebted to his wife for frequent assistance during the preparation of text and illustrations.

The great majority of the illustrations are original. They are the work of several individuals, to whom the author is grateful for hearty coöperation. Mrs. Grace Griffin Hosking is responsible for Figs. 21, 22, 26, 66, 81, 99, 135, 136, 141, 142, 144, 145, 146, 147, 149, 151, 152, 153, 157, 158, 159, 160, 161, 174, 181, 184, 185, 187, 188, 189, 196, and 216; H. C. Creutzburg for Figs. 20, 45, 47, 96, 162, 166, 167, 169, 170, 175, 177, 178, 180, 182,

186, 190, 191, 193, 209, 211, and 213; Mori Uyehara for Figs. 154 and 155; E. J. Slanetz for Fig. 18, and A. I. Weinstein for Figs. 137 and 143, as well as for Figs. 111 and 230 from his unpublished work. The other original drawings, some ninety in all, are by the author. He is indebted to Professor W. F. Ganong and the Macmillan Co. for the use of four figures from "A Textbook of Botany for Colleges"; to Professor W. F. Ganong and Henry Holt and Co. for the use of two figures from "The Living Plant," and to Dr. C. S. Gager and P. Blakiston's Sons and Co. for the use of four figures from "The Fundamentals of Botany." To the United States Forest Service, the United States Forest Products Laboratory, the Desert Laboratory of the Carnegie Institution, the Brooklyn Botanic Garden, the editors of the *Journal of Heredity* and of *Genetics,* Dr. A. J. Grout, Professors E. B. Babcock and R. E. Clausen, Dr. M. A. Howe, Professor I. W. Bailey, Professor E. W. Berry, Professor M. L. Fernald, and Professor G. S. Torrey the author is indebted for original illustrations or permission to use published ones. A few familiar figures have also been taken from some of the older texts.

The author will be very glad to welcome criticisms and suggestions, particularly those which relate to the employment of the Questions and Problems in the conduct of class work.

E. W. Sinnott.

Connecticut Agricultural College,
July, 1923.

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TO THE STUDENT

Botany has sometimes been spoken of rather slightingly as the "feminine" science, and indeed in the minds of many people it is chiefly associated with pleasant exercises in learning the names of wild flowers, or with quaint individuals who wander absentmindedly in the woods and fields, trowel and tin box in hand, and who rejoice in the use of long and unpronounceable Latin words. That such a conception of the science of botany is wholly inadequate, a study of the following pages should amply prove. Plants are far more than interesting playthings. They are a conspicuous and inescapable part of the world we inhabit. They make life possible for us by providing food, clothing, fuel, shelter, and many other necessities. More important still, they are *alive* and thus endowed with those remarkable qualities which have always made all living things eagerly studied by man, not only for their own sake but for the light which they throw on many human problems. If education is indeed an understanding of our surroundings, surely no one should pretend to be educated well who is unfamiliar with plants and their activities.

A college textbook or a college course in any branch of biology, however, ought to do something more than give familiarity with a mass of facts, no matter how important they may be. It should develop in us the *right attitude toward these facts.* This attitude—the truly *scientific* attitude—is both critical and inquisitive. It should enable us to find our way to the truth through a maze of facts. This is the attitude which distinguishes a truly educated man from one who is merely knowledge-crammed, and a lack of it is responsible for much of the loose thinking and false reasoning with regard to biological problems which is indulged in by many people.

Let us see what this attitude demands and how it may best be attained. We are all obliged to acquire a mass of information if we are to live successfully. We must know the character of the various things which we eat and wear, the operation of countless devices which we use, the rules and habits of other people, the

manifold concerns of our particular occupations, together with countless other facts and details. The world is continually asking us "*what?*", "*where?*", "*when?*" and "*how?*"; and we are continually answering it as best we may. For most people the ability to reply successfully to these questions is sufficient, and they desire nothing further. In a course in elementary botany, such would be content merely to learn the facts about plants so that they might pass the inevitable examination. There are always a few, however, who are not satisfied thus to take everything for granted, as a lesson to be learned. They want to ask the world a question in their turn, and their question is far more profound. It is "*why?*" They crave not merely knowledge but *understanding*. They want to penetrate the array of facts to the laws upon which these facts rest. To this honorable band have belonged all great thinkers and philosophers, all discoverers and explorers, all who have helped to bring mankind upward from thoughtless savagery to rational civilization. These men have often been ridiculed, frowned upon or even persecuted for their presumptuous curiosity, but they have persisted through the ages in that insatiable inquisitiveness which has led them to challenge the world, not to accept it; to penetrate its secrets rather than take all for granted. Their spirit animates every true scientist and every really educated man today.

But the scientific attitude is not mere inquisitiveness. Brutes often have plenty of that. Many people are idly curious and will accept any explanation offered them. The scientist must go beyond this. Among the many answers which come back to him when he asks "why?" he must be able to discriminate, to separate the true from the false. He must weigh accurately and without prejudice the claims of the various theories which have been put forward to answer his questions. He must remain skeptical and unconvinced until adequate proof is at hand. He must satisfy his reason. In the best sense of the word, he must be *critical*.

This attitude of critical curiosity is hard to gain and still harder to maintain actively. It is a useful practice, particularly when encountering a subject which is new or unfamiliar, to prod ourselves continually with questions and problems which it brings up, not merely accepting someone else's assertion but trying things out for ourselves. The college student, above all men, should thus learn to be his own Socrates. It is for this

purpose that the list of "Questions for Thought and Discussion," which will be found at the end of each chapter of the following text, has been gathered. The student can try his hand at these, and if he has first mastered the comparatively few facts presented in the text he should have no great difficulty. The answers to some are easy, almost obvious. Others may be harder to find but will be worth more in the finding. By frequent practice in this sort of exercise he will not only develop and keep sharp his curiosity and his ability to reason and discriminate—the most important ends for him to gain in such a course as this—but he will acquire almost unconsciously a far more thorough understanding of the structures and functions of plants than he could by merely attempting to memorize a list of facts. The tonic of curiosity and the fresh air of skepticism are sovereign aids for maintaining our minds in that state of health and vigor in which they can steadily assimilate a rich diet of knowledge without becoming sluggish and over-fed.

BOTANY: PRINCIPLES AND PROBLEMS

CHAPTER I

THE SCIENCE OF BOTANY

Botany may be defined as that field of precise and classified knowledge—that *science,* in other words—which deals with plants.

Plants and animals are distinguished from all other objects by the fact that they are *alive.* The sciences of Botany and Zoology, which treat of these two great groups of living things, are therefore closely related to one another, and deal with many facts and face many problems in common. Together they constitute the broader scientific field of Biology, which is concerned with the study of life in all its various manifestations.

Of all branches of knowledge this science of life is the least understood and in many ways the most important. Between lifeless things and living things there still exists a profound gap which modern scientific progress, great as it is, has not succeeded in bridging. Intricate mechanisms and complex chemical substances are familiar products of manufacture, but the most skillful physicists and chemists never yet have been able to construct anything alive out of non-living material, nor are they in agreement as to the details of many of the processes which go on within an organism. The structures and activities of plants and animals may be described, but often they cannot be explained. Moreover, living things are not fixed in their characteristics, but during the earth's history have undergone very great changes, evolving from simple beginnings in ages long past to the enormous variety and complexity which they exhibit today; but what was their origin, and how and why they have progressed to their present state, are questions to which biologists still can give but the vaguest of answers. It is this baffling and unexplained quality

in life which always has keenly stimulated the curiosity of man; and since he himself is a living being, much of his speculation and philosophy has naturally centered around problems which, in a broad sense, are biological in their nature. In fact, those problems of modern civilization which press most heavily for solution —food supply, race, disease, education, and many others—are concerned with the character and activities of living organisms, and the task of the biologist in adding to our scientific knowledge of plants and animals is thus by no means of theoretical importance alone, but deals with matters which are of the most vital practical interest. As an integral part of the science of biology, botany has already made notable contributions to an understanding of living things; and so long as man preserves that insatiable curiosity toward nature which has distinguished him as a thinking being, he will always in some measure be a student of plants.

Aside from its general biological interest, botany is of very direct practical importance to mankind because plants touch human activities so intimately and in so many ways. All food which nourishes animals and man and makes life possible comes originally from a union of water and a simple gas, carbon dioxide, in the leaves of green plants. Coal and oil, the chief fuels of modern civilization, have originated directly or indirectly through the activity of plants. All textile fibers are plant products or come from animals which eat plants, and the great agricultural industries themselves are merely fields of applied botany. Wood, rubber, drugs, and scores of other necessities of civilized life are plant products. Flowers and ornamental plants of many kinds play a most important part in the aesthetic life of mankind; and the natural vegetation of the earth, with its great variety and beauty, is an unfailing source of interest and satisfaction. As a means of quickening that intelligent appreciation of his surroundings which should distinguish every educated man, a knowledge of plants is therefore of the utmost value.

The Subdivisions of Botany.—Owing to the great mass of diverse facts which it has accumulated and the many points of view from which its problems have been attacked, every major science necessarily has become divided into sub-sciences, each of which makes its particular contribution to the whole. Thus botany is composed of a series of specialized sciences. Three of these—Systematic Botany, Plant Morphology, and Plant

Physiology—are most worthy of note, and are themselves subdivided and recombined still further.

Systematic Botany or *Plant Taxonomy* is concerned with the names of plants and the classification of the members of the vegetable kingdom. Its object is to identify by name and description all the kinds of plants which can be distinguished; and to arrange them, according to their natural relationships, into groups, which are called species, genera, families, and orders. Since these relationships can be determined only after a knowledge of evolutionary history, the science of *Plant Phylogeny*, which endeavors to trace the genealogy of the plant kingdom, is an important adjunct to systematic botany.

Plant Morphology is concerned with the form and structure of plants. Its object is to describe the construction and organization of the plant body and to trace underlying similarities in form between various plant groups. Under morphology are included *Anatomy*, dealing with internal structures; *Cytology*, with the structure of the cell; *Embryology*, with the development of the individual; and *Morphogenesis*, with the causes which determine form and structure.

Plant Physiology is concerned with the functions of plants. Its object is to describe and explain the various activities by which the life of the plant is maintained and transmitted to its offspring. Physiology obviously underlies the other subdivisions of botany since it touches the very process of living. A branch of physiology particularly active today is *Genetics*, which deals with the problems of inheritance.

Aside from these three major sub-sciences there are other fields of botany which deserve mention. *Plant Ecology* is concerned with the relations between plants and the various factors of their environment such as soil, climatic conditions, and living organisms; and, in particular, with the modifications of structure and function which enable them to react successfully to changes in their surroundings. Ecology necessarily involves both morphology and physiology, as well as certain of the physical sciences. *Plant Geography* is concerned with the geographical distribution of plants and the factors by which this is determined, and is related intimately both to systematic botany and to ecology, as well as to geology and geography. *Palaeobotany* is concerned with the structure and relationships of fossil plants, and thus touches systematic botany, phylogeny, morphology, and geology.

In addition to all these aspects of botany, most of which are theoretical rather than practical in their bearing, one should not fail to mention the great group of sciences concerned with the utilization and culture of plants. *Economic Botany*, in its narrower sense, is a study of those plants which are valuable to man and of the uses to which they are put. The various sciences commonly grouped under Agriculture (*Soil Science, Agronomy, Horticulture, Plant Pathology*, and many others) together with *Forestry, Pharmacology*, and their subsidiaries, are eminently practical, and their close relationship to botany is sometimes overlooked. Nevertheless they are integral parts of the science, and for their successful pursuit demand a sound knowledge of botanical principles. Everyone who is concerned with plants from a scientific point of view, whatever his purpose or profession, is rightfully to be called a botanist.

FIG. 1.—Aristotle, 384–322 B.C.

The History of Botany. *The Classical Period.*—The botany of today is the result of a long period of progress and development. It looks back, as do so many other sciences, to the fertile speculations of the Greeks for the first definite expression of its problems and principles. The "nature" of plants was studied by Aristotle

(384-322 B.C., Fig. 1), who saw clearly certain of the broader problems of plant and animal life, and whose sagacious comments thereon are still worthy of attention. As the teacher and friend of Alexander the Great, he was in a particularly favorable situation to receive specimens and descriptions of the plant and animal life of most of the world then known, and he was the first man to become familiar with a wide range of biological facts. It is his disciple Theophrastus of Eresus (371-287 B.C.), however, whom botanists have generally regarded as the father of their science. This keen naturalist accumulated a great mass of information with regard to plants and discussed their various characteristics. Rome also had her share in the development of plant science, notably through the contributions of Pliny the Elder (23-79 A.D.), whose "Natural History," a compendium of facts and fancies about living things, was long a storehouse of botanical information. Dioscorides, living at about the time of Nero, studied plants for their medicinal properties and holds an important place historically both in botany and in medicine.

The Herbalists.—After this, its classical period, botany went into that profound eclipse suffered by all sciences during the Middle Ages. The teachings of the ancient masters were jealously preserved and were commented upon and dissected, but the idea of extending knowledge by direct observation and experiment was held to be almost sacrilegious. About the beginning of the sixteenth century, however, a group of botanists living in the Rhine valley and its adjacent regions undertook to explore the plant kingdom afresh for themselves. They were interested in plants chiefly for the curative virtues to be found therein and, paying scant attention to the doctrines and dogmas of the ancients, they went about describing and drawing with fidelity the various kinds of plants which flourished in their native countries. From the numerous herb-books or "herbals" (Fig. 2 and Frontispiece) in which the resulting discoveries were published, these pioneers have been known as the "Herbalists." They endeavored to distinguish clearly the different species from one another, and proposed certain crude methods of classifying the plant kingdom. So unprejudiced and free from the conventional dogmatism of the age was their whole attitude that the Herbalists are generally regarded as the founders of modern botany.

The Modern Period.—The first extensive and thorough classification of plants was that proposed in 1583 by the Italian bota-

TOMVS Tertius. 29

Herba Sanctę TRINITATIS.

Dreyfaltigkeit blům.

¶ De herba Sanctæ TRINITATIS.

Teutonice / Dreyfeltigkeit blům.

RHAPS. V.

HErba, quam noſtri a triplici colore floris, nomine Trinitatis donauerunt, coronaria eſt, & ob id paſſim in hortis plantata.

IVVAMENTA ex aqua diſtillationis illius.

Aqua ex ea diſtillata, pueris in potum exhibita, inordinatos illorū calores reſtinguit.

Prodeſt & Aſthmaticis, qui anguſtias in præcordijs ſentiunt, pulmonumqꝫ apoſtematibus ſingulari præſidio eſt.

Cæterum quo nomine a Dioſcoride cenſeatur, hactenus incompertum habeo: tametſi quibuſdam Iaceam uocari placet.

C 3

FIG. 2.—A page from the herbal of Otto Brunfels, published in 1532 (see Frontispiece). The appearance, description, and medicinal virtues of the pansy are here set forth.

nist Cesalpino (1519–1603). Combining an acquaintance with the ancients and an intimate first-hand knowledge of plants, he laid down certain principles which were the basis of systematic botany for many years. Modern taxonomy, however, dates from the publication of the "Species Plantarum" by the great Swedish naturalist Linnaeus (1707–1778, Fig. 3), in 1753. In this monumental book all the plant species known at that time were named, carefully described, and arranged according to a definite system.

FIG. 3.—Carolus Linnaeus (Carl von Linné), 1707–1778.

Although the early work in botany was thus concerned chiefly with taxonomy, the study of plant structures was not neglected. Grew (1628–1711) in England, and Malpighi (1628–1694) in Italy, were keenly interested in the internal construction of the plant body, and their works on "phytotomy" laid the foundation for modern knowledge of plant morphology. The continued improvement in the compound microscope made possible more complete and accurate knowledge of the way plants are constructed, and led to the formulation by Schleiden, in 1838, of the Cell Theory, which states that the cell is the unit of structure in plants and that protoplasm is its essential constituent. From this beginning, modern anatomy and cytology have added a great body of facts to our knowledge of the structure, growth, and reproduction of the plant body.

The ancients and the early modern botanists for the most part had fanciful and inaccurate ideas as to the way in which the plant carried on its various functions, an ignorance largely due to the undeveloped state of the sciences of physics and chemistry in their times; and it was not until the latter part of the eighteenth century that modern plant physiology became definitely established. Oxygen was discovered by Priestley in 1774, and five years later a Dutch physician, Ingenhousz, observed that green plants in the light take in carbon dioxide and give off oxygen, and that all plants give off a certain amount of carbon dioxide.

FIG. 4.—Charles Darwin, 1809–1882.

These gas exchanges were measured accurately by de Saussure in the early years of the nineteenth century, and some of the important principles of plant physiology thus became established. Since that time the development of modern chemistry and physics has made possible a steady advance in knowledge of the physiological processes of living things.

The publication of the "Origin of Species" by Charles Darwin (Fig. 4) in 1859 resulted in a general acceptance among scientists of the theory of evolution. A recognition of the fact that the plants of today have been developed slowly from simpler ancestors has had a profound effect upon botanical science and has stimulated a great interest in reconstructing the "family tree" of the plant kingdom and establishing a really "natural"

system of classification, based on actual relationship, to replace the artificial systems of Linnaeus and his predecessors. It has also led to a more intensive study of the laws of variation and inheritance, and the causes and method of evolution. This has been encouraged still further by the discovery of Mendel's laws of inheritance, propounded in 1866, disregarded for many years, and finally brought to the attention of biologists again in 1900.

The present state of the science of botany, then, is the result of a long period of slow development, in which truth has been gradually separated from error and the present vast store of facts amassed. Hundreds of investigators in institutions of learning, government experiment stations, and other research agencies, are studying plants from every point of view and each year sees an array of new facts added to previous knowledge of the subject. Many problems have been successfully solved, and progress is steadily being made upon others. With each advance, new questions have arisen and new fields of investigation have opened, until botanical science has broadened from a mere discussion of the names and properties of medicinal herbs to an attack upon the fundamental problems of life itself.

QUESTIONS FOR THOUGHT AND DISCUSSION

1. In what important ways do living organisms differ from lifeless objects?

2. Name three important differences between a typical plant and a typical animal.

3. What relation can you suggest between the fact that animals are unable to manufacture their own food and the fact that they have a much more highly developed nervous system than do plants?

4. Could mankind get on better without domestic animals or without cultivated plants? Explain.

5. Civilization usually has developed to a higher level in agricultural countries than in pastoral ones. Explain.

6. What is the most important contribution made by plants to man's welfare?

7. In what respects might the following be regarded as botanists?

A farmer	A florist
A forester	A furniture-maker
A physician	A landscape architect
A druggist	A geologist

The ancients and the early modern botanists for the most part had fanciful and inaccurate ideas as to the way in which the plant carried on its various functions, an ignorance largely due to the undeveloped state of the sciences of physics and chemistry in their times; and it was not until the latter part of the eighteenth century that modern plant physiology became definitely established. Oxygen was discovered by Priestley in 1774, and five years later a Dutch physician, Ingenhousz, observed that green plants in the light take in carbon dioxide and give off oxygen, and that all plants give off a certain amount of carbon dioxide.

FIG. 4.—Charles Darwin, 1809–1882.

These gas exchanges were measured accurately by de Saussure in the early years of the nineteenth century, and some of the important principles of plant physiology thus became established. Since that time the development of modern chemistry and physics has made possible a steady advance in knowledge of the physiological processes of living things.

The publication of the "Origin of Species" by Charles Darwin (Fig. 4) in 1859 resulted in a general acceptance among scientists of the theory of evolution. A recognition of the fact that the plants of today have been developed slowly from simpler ancestors has had a profound effect upon botanical science and has stimulated a great interest in reconstructing the "family tree" of the plant kingdom and establishing a really "natural"

system of classification, based on actual relationship, to replace the artificial systems of Linnaeus and his predecessors. It has also led to a more intensive study of the laws of variation and inheritance, and the causes and method of evolution. This has been encouraged still further by the discovery of Mendel's laws of inheritance, propounded in 1866, disregarded for many years, and finally brought to the attention of biologists again in 1900.

The present state of the science of botany, then, is the result of a long period of slow development, in which truth has been gradually separated from error and the present vast store of facts amassed. Hundreds of investigators in institutions of learning, government experiment stations, and other research agencies, are studying plants from every point of view and each year sees an array of new facts added to previous knowledge of the subject. Many problems have been successfully solved, and progress is steadily being made upon others. With each advance, new questions have arisen and new fields of investigation have opened, until botanical science has broadened from a mere discussion of the names and properties of medicinal herbs to an attack upon the fundamental problems of life itself.

QUESTIONS FOR THOUGHT AND DISCUSSION

1. In what important ways do living organisms differ from lifeless objects?

2. Name three important differences between a typical plant and a typical animal.

3. What relation can you suggest between the fact that animals are unable to manufacture their own food and the fact that they have a much more highly developed nervous system than do plants?

4. Could mankind get on better without domestic animals or without cultivated plants? Explain.

5. Civilization usually has developed to a higher level in agricultural countries than in pastoral ones. Explain.

6. What is the most important contribution made by plants to man's welfare?

7. In what respects might the following be regarded as botanists?

A farmer	A florist
A forester	A furniture-maker
A physician	A landscape architect
A druggist	A geologist

8. In what field of botany are the following investigators at work. students of (*a*) stem structure in the wheat plant; (*b*) the geographical distribution of species of wheat; (*c*) the rate of food manufacture in wheat plants; (*d*) the classification of wheat species; (*e*) wheat breeding; (*f*) the minute structure of the cells of wheat plants?

9. State some very specific problem relating to plants and of practical importance in agriculture or any other industry (a problem such as might be under investigation by an expert in the United States Department of Agriculture, for example) in the solution of which a knowledge of plant taxonomy would be valuable.

10. Name such a problem in which a knowledge of plant morphology would be valuable.

11. Name such a problem in which a knowledge of plant physiology would be valuable.

12. Name such a problem in which a knowledge of plant genetics would be valuable.

13. Name such a problem in which a knowledge of plant ecology would be valuable.

14. Give an instance of a practical situation in which a man with a knowledge both of botany and of practical agriculture would have an advantage over a man who knew only the latter. Why does he have this advantage?

15. How is a knowledge of chemistry important to a botanist?

16. How is a knowledge of physics important to a botanist?

17. How is a knowledge of meteorology important to a botanist?

18. How is a knowledge of geology important to a botanist?

19. Why was systematic botany the first aspect of botany to be studied scientifically?

20. Plants always have been used far more for food than for medicine, but despite this fact the science of botany in its early days was almost entirely in the hands of men interested in medicine rather than in agriculture or any other branch of practical science. How do you explain this?

21. Why was a knowledge of the minute structure of plants impossible for the ancients to acquire?

REFERENCE PROBLEMS

1. Name some of the notable herbalists, and give a brief account of the life and work of each.

2. Name three American botanists of the nineteenth century and give a brief account of the life and work of each.

3. What is the largest and most important Botanical Garden in the world? Give a brief account of its history and activities.

4. Name the various governmental agencies in this country which are carrying on botanical investigations.

5. The following "applied" sciences are all closely related to botany and are founded upon it. With what does each deal?

Horticulture	Forestry
Agronomy	Plant Pathology

6. Summarize the life and work of Aristotle and enumerate his important contributions to botany.

7. Summarize the life and work of Linnaeus and enumerate his important contributions to botany.

8. Summarize the life and work of Darwin and enumerate his important contributions to botany.

9. What change in geological theory occurred at about the same time that the theory of evolution won wide acceptance (in the latter half of the nineteenth century)?

10. Give the author and title of three important books dealing with the history of botany, and outline briefly the content of each.

11. Give the derivation of the following terms and explain in what way each is appropriate:

Taxonomy	Physiology	Ecology
Morphology	Phylogeny	Genetics

CHAPTER II

INTRODUCTORY SURVEY

Before commencing an intensive study of any aspect of botanical science or of any particular problem which deals with plants, it will be well to make a brief survey of the plant kingdom as a whole, and of some of the more important structures and functions of plants in general.

The Plant Kingdom.—About 250,000 different kinds or *species* of plants have been discovered and described, and every year botanical exploration and careful study bring more of them to knowledge. The problem of systematic botany is to name this host of plants and to arrange and classify its members in a logical system. This is a task of great difficulty in view of the enormous number of species, the great diversity of size and structure which they exhibit, and the wide range of environmental conditions to which they have become adapted. The crude systems of classification of the earlier taxonomists have been modified and refined, and through the application of facts derived from practically all fields of botany, a modern and scientific system of classification is gradually being established. Over many of the details of such a classification differences of opinion still exist, but there is now a rather general agreement as to the major groups into which the plant kingdom should be divided. Four main divisions are commonly recognized:

The Thallophytes.—These are lowly plants, various in their structure, activities, and methods of reproduction, but agreeing in the possession of a simple body without roots or leaves and in multiplying by minute single-celled *spores*. The majority of Thallophytes inhabit water or moist places, and are small, inconspicuous, and soft-bodied plants. The group as a whole is much less homogeneous than the other three divisions, and many of its members have nothing more than a distant relationship to each other.

There are two main series of Thallophytes: The *Algae* (Fig. 5), which possess the green pigment *chlorophyll* and are thereby

able to manufacture their own food, and which include all the seaweeds and their fresh-water allies; and the *Fungi* (Fig. 6), which lack chlorophyll and consequently are obliged to obtain their food from living animals and plants or from dead organic material. To the latter group belong the vast array of bacteria, molds, blights, rusts, toadstools, mushrooms, and similar plants, many of which live as parasites and are often the cause of serious diseases of man and the lower organisms.

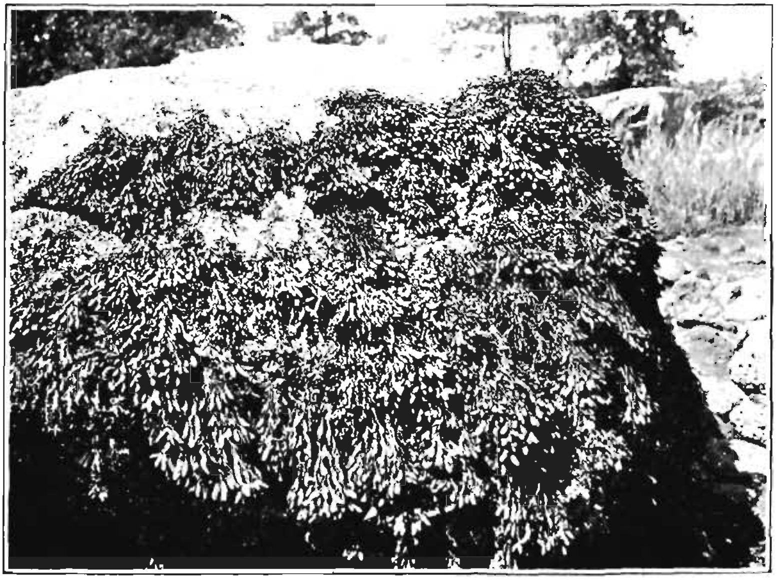

FIG. 5.—An alga. One of the rock-weeds (*Fucus spiralis*) growing on a rock between tide-marks. (*Photo by M. A. Howe.*)

The Bryophytes, or Moss Plants.--These plants are distinguished from the Thallophytes chiefly by their more highly developed sexual structures and their more complicated methods of reproduction. The plant body of the Bryophytes has no roots, and in many cases consists of only a flat, strap-like mass of green tissue, though the higher members of the group possess very simple stems and leaves. The plants are small and inconspicuous, and generally thrive best in situations where water is abundant. Bryophytes are subdivided into the simple and lowly *Liverworts* (Hepaticae) and the commoner and more highly specialized *Mosses* (Musci, Fig. 7).

The Pteridophytes, or Fern Plants.—These possess true roots, stems, and leaves, essentially similar in structure to those of the Seed Plants, but they reproduce by spores rather than by seeds. Compared with that of the Bryophytes, the plant body is large and vigorous, and it is well adapted to life on land. The three

FIG. 6.—A fungus. One of the gill fungi, *Pleurotus*, growing on a log.

important subdivisions of the Pteridophytes are: the *Ferns* (Filicales, Fig. 8), possessing large and feathery leaves on the backs of which the spores are produced; the *Club Mosses* or *Ground Pines* (Lycopodiales), which have spore-bearing cones, solid stems, and scale-like, spirally arranged leaves; and the *Horsetails* (Equisetales), also possessing cones, but with jointed, hollow stems and minute, whorled leaves.

The Spermatophytes, or Seed Plants.—The dominant and familiar portion of the earth's vegetation today consists of these

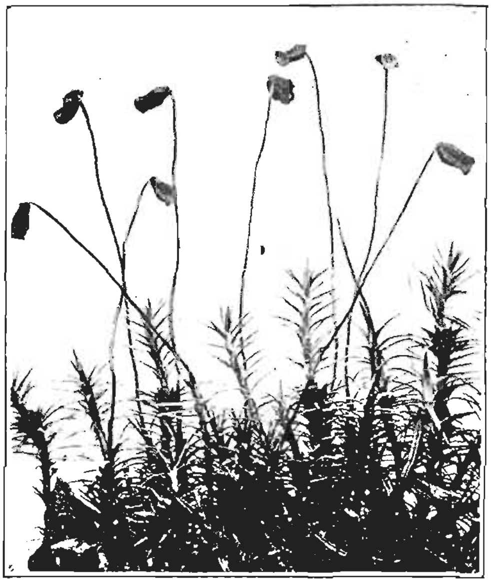

FIG. 7.—A moss. A hair-cap moss (*Polytrichum juniperinum*) with ripe capsules. (*From A. J. Grout, "Mosses with Lens and Camera." Copyright by the author.*)

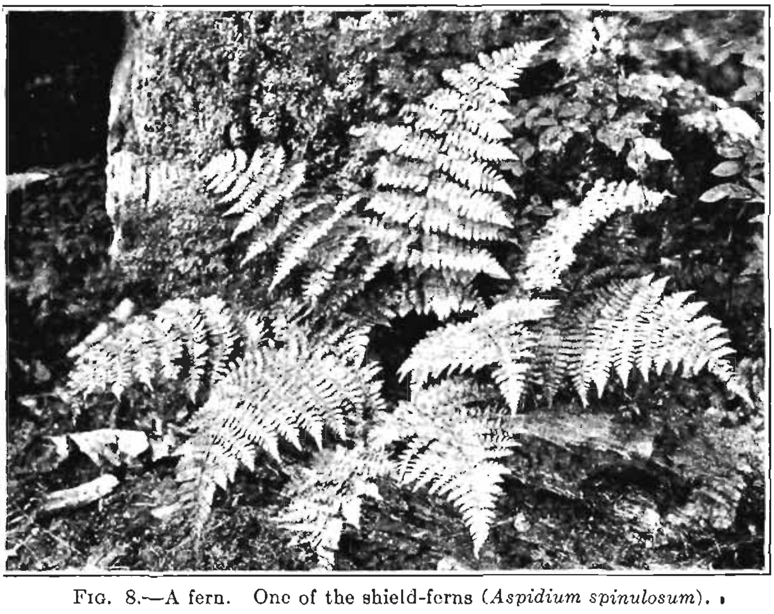

FIG. 8.—A fern. One of the shield-ferns (*Aspidium spinulosum*).

plants, which are well adapted for life on land and often attain great size. Their distinctive feature is the production of a complex, many-celled reproductive body, the *seed*, which con-

FIG. 9.—A seed plant (Gymnosperm). Fir tree (*Abies nobilis*).

sists of an embryo plant provided with a supply of stored food and wrapped in a protective coat.

Seed Plants are very numerous and exceedingly varied in form and structure, ranging from small and delicate herbs to huge trees over three hundred feet tall. They are the most conspicuous and best known of all the divisions of the plant kingdom, and

provide the great bulk of the foods, timbers, fibers, and other vegetable products so important to civilized man.

FIG. 10.—A seed plant (Angiosperm). Hawthorn tree (*Crataegus*).

Two major subdivisions of the Seed Plants are recognized: the *Gymnosperms* (Fig. 9), which have primitive, often cone-like flowers and bear their seeds openly exposed on scales, as in

the common coniferous trees; and the *Angiosperms* (Fig. 10), in which there is usually a typical flower with its various floral parts, including an *ovary* in which the seeds are enclosed during their development. There are only about 450 species of Gymnosperms living today, but the Angiosperms are an enormous group of more than 130,000 species. They are divided again into two main groups, the *Dicotyledons* and the *Monocotyledons*, which differ from each other in the structure of the seed, leaf, stem, and flower.

Underlying the differences by which these various groups are distinguished from one another there are many fundamental similarities in structure and function which are common to all plants; but the marked changes which appear as one passes from the lowest to the highest types make very difficult a concise description of the characteristics of the plant kingdom as a whole. It will therefore be profitable to confine attention, at first, mainly to those plants which are familiar to everyone and of most obvious and immediate interest to man—the Seed Plants; and the sciences of morphology and physiology, as exemplified by the Seed Plants, will thus be the chief objects of study in the first portion of this book. In these early chapters one should be careful, therefore, to remember that only one division of the plant world—albeit the most important one—is being considered, although many of the facts and principles there established are, of course, valid for all plants. In the last chapters of the text there will be discussed in some detail the lower members of the vegetable kingdom, and the respects in which they differ from each other and from the Seed Plants.

The great variety of plant types and the diversity of conditions under which they live renders it difficult to make general statements about plants which are universally true, for exceptions to almost any such statement can usually be found. Indeed, variability is one of the most notable characteristics of all living things. The student should therefore bear in mind that many of the facts and principles set forth briefly and simply in an elementary text are to be taken as true for typical cases and under ordinary conditions, and he should be careful not to accept them as necessarily and universally true for all plants and under all conditions. Living organisms are too complicated to be described completely in simple formulas.

The Structures and Functions of Plants.—A notable characteristic of plants, which they share with all other living things, is

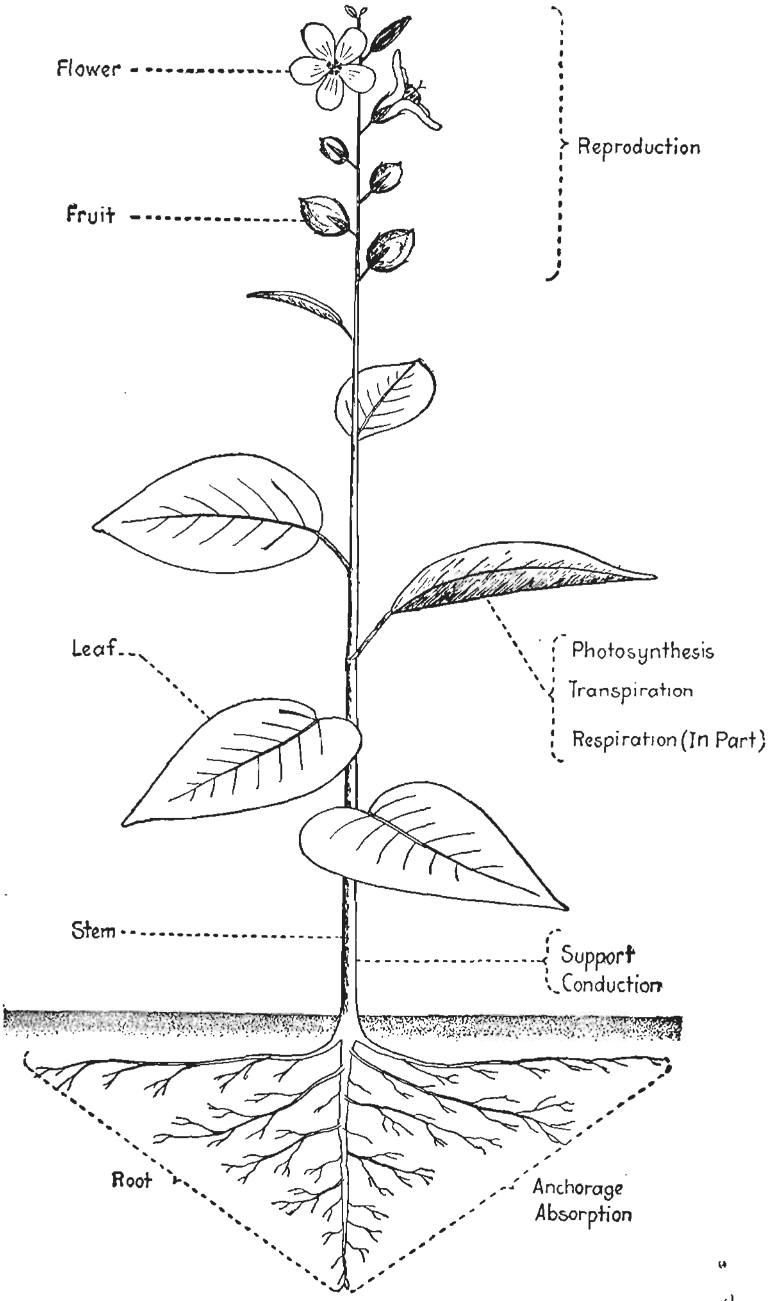

FIG. 11.—The important structures and functions of a seed plant, illustrated diagrammatically.

their very definite bodily form. This form is not merely external or accidental but is the mark of a fundamental organization or "division of labor" within the plant itself. The individual is made up of a series of distinct and visibly different parts, each of which possesses a specific shape and performs a specific function (Fig. 11). These parts are called *organs*. The root, the stem, the leaf, the flower, the fruit, and the seed, as well as the various subordinate parts of which each may be composed, such as bud, petiole, or stamen, are some of these organs.

The organ, in turn, is not homogeneous in texture and construction but is made up of a group of *tissues*, each of which performs a particular task contributory to the general function of the entire organ. Thus a stem may be composed of bark tissue, cortical tissue, phloem tissue, cambial tissue, woody tissue, and pith tissue, each of them playing some role in the economy of the stem as a whole. One type of tissue, of course, may enter into the construction of several organs, as does woody tissue, for example, in the root, the stem, and the leaf.

A tissue, in turn, is an aggregation of *cells*, those ultimate units of structure and function in all organisms. Each plant cell is a minute but distinct bit of living substance, or *protoplasm*, with nucleus, plastids, sap cavity, and other structures of its own, and is usually enclosed in a cellulose wall. The individual plant, indeed, may be regarded as a huge colony of minor individuals, the cells, each performing some particular function in the whole and all bound together to their mutual advantage. A knowledge of the structure and activities of living cells is the foundation upon which an understanding of plants and animals must be built.

This differentiation of the plant body into a series of specialized structures is found, of course, only in the higher plant groups. Among the lowest and simplest forms the entire body is a single cell, but this is capable of carrying on a wide range of functions. Somewhat more complex types consist of a group of cells and in still higher ones the beginnings of specialization occur. The complex and highly differentiated body of one of the familiar seed plants is the result of a long process of evolutionary advance.

The Root and Its Functions.—The root is that organ which anchors the plant in the soil and absorbs therefrom water and simple inorganic nutrient materials. Aside from these primary functions, it frequently serves as a storehouse for reserve food and

often assumes other secondary duties. The root system may consist of a single strong *tap root*, with weak lateral branches, or of a much-branched series of smaller *fibrous roots*. The function of absorption takes place in minute root hairs, delicate outgrowths from the surface cells just behind the young and growing root tip. Into these root hairs, by the process of *osmosis*, pass water and dissolved substances (chiefly nutrient mineral salts) from the soil.

The Leaf and Its Functions.—The typical leaf is a broad and thin structure, green in color and freely exposed to air and light. Its essential portion, the *blade*, is usually supported by a stalk, the *petiole*. Most of the internal cells of the leaf possess a green pigment, *chlorophyll*, which can utilize the energy of light to combine the gas carbon dioxide (coming from the air) with water (coming from the soil) into *grape sugar*, a simple carbohydrate food. This process of *photosynthesis* is confined entirely to green plants. By it is manufactured all the food which sustains the life not only of plants but of all animals and of man himself, for all the various foods familiar in animal nutrition have been built up by progressive modifications of grape sugar produced in green leaves. Because of this unique food-making ability, green plants are thus essential to all the rest of organic nature.

The leaf blade is provided with conducting channels or *veins* which carry water and salts from the soil into the leaf and transport therefrom the products of photosynthesis. A protective *epidermis* surrounds the whole and is provided with pores or *stomata*. Water coming up the stem from the roots evaporates from the internal tissues of the leaf and passes out through the stomata in the process of *transpiration*.

The Stem and Its Functions.—The primary function of the stem is to hold the leaves out into the light where they may carry on photosynthesis successfully. It must thus have considerable mechanical strength, particularly in tall plants, and it must also be able to serve as a highway for the transportation of materials between roots and leaves. The ascent of water and mineral nutrients takes place chiefly in a specially modified tissue, the *wood;* and the translocation of food from the leaves to other parts of the plant is carried on through the *phloem*. The stem is also important as a means for supporting the flowers in positions where they may be pollinated readily. Stems may be com-

paratively small and soft as in herbaceous plants, or stout and woody as in trees and shrubs. They are occasionally modified for special functions, such as food-storage or photosynthesis.

The Reproductive Organs and Their Function.—The root, leaf, and stem are all concerned with the *vegetative* activities of the plant. The production of offspring, through which the life of the plant may be transmitted to succeeding generations, is the function of the *reproductive* organs. The *flower,* typically composed of *sepals, petals, stamens,* and *pistil,* is concerned with effecting *fertilization,* or the union of male and female sexual cells; the *fruit* protects the growing seeds and often aids in their dispersal; and the *seeds* are young plants themselves in embryo, protected by a coat, provided with a supply of food, and ready to begin their independent growth and development whenever favorable conditions appear.

Metabolic Processes.—Certain physiological activities of the plant are not confined to any one organ but are characteristic of living protoplasm wherever it may be. Notable among these are *digestion,* whereby food is rendered soluble; *assimilation,* whereby such digested food is incorporated into protoplasm, and *respiration,* whereby the supply of energy necessary for the plant's activities is released through the breaking down of living tissue, with the consequent absorption of oxygen and liberation of carbon dioxide.

QUESTIONS FOR THOUGHT AND DISCUSSION

22. There are almost as many species of Thallophytes as of Seed Plants, but the latter are much more familiar to most people than are the former. Explain.

23. Which of the four main divisions of the plant kingdom do you believe is the oldest? Explain.

24. Which of these four divisions contains the most plants useful for food? the largest plants? the smallest plants?

25. To which of these four divisions do plants growing in the ocean chiefly belong? To which do land plants chiefly belong?

26. Name some Thallophytes which are useful to man and some which are harmful.

27. Name some Spermatophytes which are useful and some which are harmful.

28. Which of the four divisions do you think contains the largest number of plant species which are harmful to man and to his domestic animals and plants? Which contains the largest number of useful species?

29. Bryophytes and Pteridophytes have many fewer species than either Thallophytes or Spermatophytes. What reason can you suggest for this fact?

30. What are the advantages of organization (the "division of labor") in a plant?

31. Which of the four main divisions of plants shows the highest degree of organization within its plant body?

32. In general, has it been the most highly organized or the least highly organized plants which have been most successful? Explain your answer.

33. Why are living things called "organisms"?

34. Roots are confined almost entirely to land plants. Explain.

35. Give an example of a root which serves as a store-house for a large amount of food.

36. What advantage has the root over the stem as a place for food storage?

37. Name as many cultivated plants as you can in which the root is the organ useful to man.

38. Name a few plants in which the stem is very much reduced. Under what important disadvantage are such plants?

39. Name as many cultivated plants as you can in which the stem is the organ useful to man.

40. The blade of an ordinary leaf is broad and thin. Explain the advantage of this to the plant.

41. Name as many cultivated plants as you can in which the leaf is the organ useful to man.

42. What makes reproduction necessary among living things?

43. Name ten cultivated plants in which the fruit or seed is the organ useful to man.

44. Are the most important agricultural crops derived from the root, the stem, the leaf, or the fruit? Explain.

45. What important resemblances are there between the physiology of a typical plant and of a typical animal? What important physiological differences are there between these two groups of organisms?

REFERENCE PROBLEMS

12. How does the number of plant species in the world compare with the number of animal species?

13. Name some seed plants which lack true roots; which lack leaves; which lack a stem; which lack functional flowers.

14. Outline briefly what appear to have been the main steps in the evolutionary history of the plant kingdom, as indicated by evidence from living and fossil plants.

15. Give an account of the character and content of Engler and Prantl's "Natürlichen Pflanzenfamilien."

16. Give author and title of five of the older and "classic" text books of botany (such as those by Sachs, Strasburger, and Gray) and outline briefly the content of each.

17. Give the derivation of the following terms and explain in what way each is appropriate:

Thallophyte Bryophyte Pteridophyte
Spermatophyte

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CHAPTER III

THE CELL

The remarkable advance which all the sciences have made during the past two centuries has not been due to any general increase in the ability and intelligence of scientists themselves, but has followed the development of some marked advances in methods of observing the facts of nature. The telescope, the microscope, the spectroscope, and many similar instruments which are of relatively recent invention or perfection opened to scientific investigation a very wide range of phenomena with which man had previously been entirely unfamiliar. This broadening of the scientific horizon has nowhere been more notable than among the biological sciences. The earliest botanists, for example, could become acquainted with the general external structure of the plant, and through their dissections were able to gain some idea of the disposition of its tissue systems; but not until Robert Hooke studied a thin slice of cork with his crude microscope in 1665 and found it to be composed of tiny "cells" did they begin to suspect that plants might have a minute structure worthy of investigation. Even then many years passed before the full importance of cells was recognized, and not until well along in the nineteenth century was it definitely established that all plants are composed of minute units of living material, and that the structure and functions of plants can be understood only through an adequate knowledge of these living cells themselves. Just as chemical facts can best be interpreted through an acquaintance with the properties and behavior of atoms, so the structure, growth, and physiological activities of plants and their organs can be understood only through the study of the minute cells which compose them. It is therefore necessary, before one can hope to gain more than a superficial knowledge of any particular plant structure, to devote some attention to the structure and organization of cells.

The Plant Cell.—All cells are very small objects, the largest barely visible to the naked eye, and some of the smallest so minute

that very high powers of the microscope are required to distinguish them. Cells which compose ordinary plant tissue vary approximately from .1 to .01 of a millimeter in diameter, so that from 20 million to 20 billion would be contained in a cubic inch! An ordinary leaf consists of many millions of cells, and a tree obviously contains countless billions. It is hard to think in terms of such very small objects, and one of the difficulties which a botanist must encounter is to carry over into his ordinary experience of plants the facts which the microscope shows him as to their minute structure.

The objects which Hooke first called "cells" were merely the cellular cavities in dead cork; and similar cavities were found in wood and many other plant structures. A wider study soon showed that in living tissue such cavities were filled with various substances; and it was found that one particular kind of material, liquid or jelly-like in character, was always associated with the activities commonly called "life," and hence was recognized as the ultimate *living material.* To this the name *protoplasm* was given; and the essential features of the Cell Theory, as formulated by Schleiden and Schwann in 1838, is that living things are made up of minute but distinct bits or units of protoplasm. These units, rather inappropriately, thus came to be called *cells.* The term *protoplast* is a much more accurate one, but the older word has been used so widely that it probably will never be displaced.

Plant cells are of many types and perform a great variety of functions, but there are certain characters which most of them have in common (Fig. 12). Their protoplasm is not homogeneous, but consists of a denser, more or less spherical *nucleus,* with a complex internal structure of its own; and a less dense mass, the *cytoplasm,* in which may occur various minute bodies. In mature and functioning cells, the cytoplasm is usually pressed closely to the wall in a thin film, and the center of the cell is occupied by a *vacuole* or *sap cavity,* filled with water in which various substances are dissolved. Around the cell is secreted a wall of dead material, consisting chiefly of cellulose.

Protoplasm.—All the various processes which go on in the body of the plant, such as the absorption of water and salts, the manufacture of food, digestion, respiration, growth, and reproduction—processes which in the aggregate are called "life"—are ultimately directed and controlled by the remarkable material, protoplasm, which constitutes the essential part of every

living cell. For this reason protoplasm is regarded as the only part of an organism which is truly alive, and a knowledge of its structure and activities is therefore essential for an understanding of any living thing. Indeed, if one could comprehend thoroughly a bit of this material, he would be in a fair way to understand all living things. Every problem of life in its last analysis is a problem of protoplasm.

The physical construction and the chemical composition of protoplasm have been studied intensively in an endeavor to explain its remarkable properties, but although such investigations have been conducted with the aid of every modern refinement of analysis, and although they have disclosed many important facts as to protoplasmic structure and activity, it must nevertheless be admitted that they have not yet yielded a knowledge of the fundamental chemical or physical organization of this material adequate to explain its characteristic "living" behavior.

Physical Properties.—Physically, ordinary protoplasm is a rather thick liquid somewhat resembling egg white in its visible properties, rather elastic, and with about the consistency of glycerine. It may be considerably thinner or thicker than this, and is often gelatinous. It varies widely in different parts of the plant and under different conditions. With even the highest powers of the microscope protoplasm appears as a clear liquid, the *hyaloplasm*, in which are suspended minute granules and globules of various sizes, types, and abundance. All these visible inclusions, however, may be removed without changing the characteristic properties of protoplasm, which therefore seem to lie in the apparently structureless portion itself.

Protoplasm a Colloidal System.—Perhaps the most important physical fact about protoplasm is that it belongs to that group of structures which are in a *colloidal* condition. Such substances, whether solids, liquids, or gases, are in an exceedingly fine state of subdivision, and are suspended in an enveloping medium which itself may be solid, liquid, or gaseous. Thus there are various types of colloidal systems, such as solids in liquids, solids in gases, liquids in gases, liquids in liquids, gases in liquids, and so on. Jelly, egg albumen, glue, and fine emulsions (such as mayonnaise dressing) are common examples. The suspended particles may be large enough to be seen under the microscope but are often much smaller, though still large in comparison with particles of molecular size which enter into true solutions. The surface

exposed by these minute particles is very great. If a cubic centimeter of starch, for example, is divided into particles of colloidal size, such as occur in starch paste, these have an aggregate surface of about sixty square meters, or 100,000 times as much as that of the solid cube. This enormous surface necessarily has an important influence on the reactions which go on within colloidal systems.

Colloids are subject to marked alterations which may be brought about by very slight changes in composition. An emulsion of oil in water, for example (fine droplets of oil suspended in water) may be reversed into an emulsion of water in oil by a slight chemical change, and the balance between these two states may be extremely delicate. A colloid in which the particles are relatively free to move (a "sol") may also pass over into a semi-solid gelatinous state, or "gel," and back again. The coagulation of a colloid (of which the coagulation of egg white on cooking is an example) is gelation which is not reversible in this way. In general, colloids are not soluble in the true sense, do not crystallize, are more viscous than water, coagulate easily, are poor conductors of electricity, and have little or no osmotic effect.

The extreme complexity and instability which a colloidal system may attain suggest that the great variety of reactions carried on continually in protoplasm may be associated in some way with its colloidal character. Just what type of colloidal structure living material has, however, is not known, but it is probably an emulsion, the suspension of minute droplets of liquid within another liquid. Protoplasm is by no means a simple emulsion, but seems to be a far more heterogeneous colloidal system, probably including several types of colloidal structure, together with much material in true solution. Biologists are coming to the opinion, however, that the mere complexity of its physical construction, much as this may facilitate the complexity of its functions, is not the essential characteristic of protoplasm, but that what causes it to carry out the remarkable regulatory activities in which life consists is rather some definite type of chemical or physical *organization,* the analysis of which has thus far eluded discovery.

Chemical Properties.—Chemical analysis is equally disappointing in giving an ultimate understanding of protoplasm. Perhaps the most important fact yielded thereby is the very large amount of water which protoplasm contains. This usually

constitutes about 80 per cent of the weight of living material, and may go as high as 95 per cent. Water is essential to all living things, for physiological processes in plants and animals are carried on in solutions, and the maintenance of a sufficient supply of water for these processes is consequently of the utmost importance.

The remainder of the protoplasmic substance consists chiefly of proteins, that group of organic compounds which are composed of carbon, hydrogen, oxygen, and nitrogen. These often contain sulphur and phosphorus as well, the latter element being particularly important as a constituent of the nucleus. Fats, sugars, and various mineral salts are also present. Proteins, however, are the characteristic components of protoplasm; but a satisfactory chemical analysis of these most complex of all organic substances, particularly as they exist in the living cell, seems impossible to obtain. The great variety, complexity, and instability of these proteins is another factor in the remarkable intricacy of living material in general.

The Nucleus.—The protoplasm of a cell is not homogeneous, but contains within it a number of specialized structures, chief among which is the nucleus (Fig. 12, N). This is an approximately spherical body, markedly denser than the rest of the protoplasm, and bounded by a definite membrane. The nucleus is evidently the directing center for the more important physiological activities of the cell, such as the synthesis, digestion, and assimilation of foods, the formation of the cell wall, cell division, growth, and the transmission of hereditary traits in reproduction.

That the nucleus is essential in these various functions has been proved in a number of different ways. Cells from which the nucleus has been removed artificially will often live for a time, but fail to carry on actively their normal metabolic processes, suggesting that the nucleus produces and secretes into the rest of the cell enzymes and other substances which regulate and control its activity. A study of cell division (which will be considered in a later chapter) shows clearly that this process is also initiated and carried out primarily by the nucleus. Finally, experiments in the inheritance of traits in plants and animals indicate that in all probability the hereditary material which an offspring receives from its parents is actually transmitted by the chromosomes, minute bodies within the nucleus.

The bulk of the nucleus consists of a clear liquid, the *nuclear*

sap. Imbedded in it is a network of denser material, the *reticulum.* Portions of this are relatively thin and are sometimes known as the *linin;* other portions, which are thicker and can be stained very easily, are called the *chromatin,* though the distinction between these two materials often is not a sharp one. At cell division this nuclear network becomes aggregated into definite

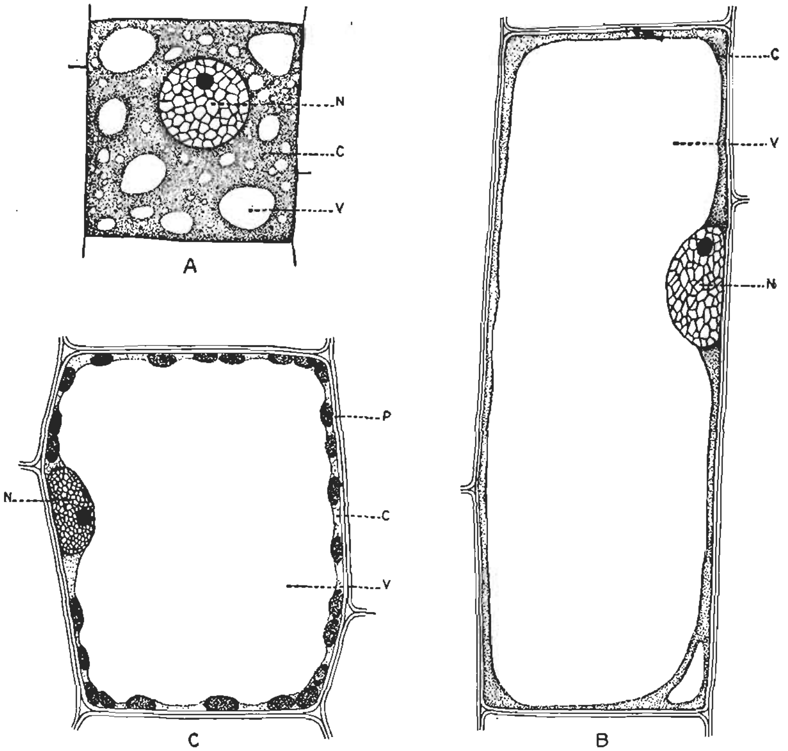


FIG. 12.—Plant cells. *A,* young cell from a growing region; *B,* mature cell developed from *A*; *C,* chlorophyll-bearing cell. N, nucleus; C, cytoplasm; V, vacuole; P, plastid.

bodies, the *chromosomes,* which behave in a very characteristic manner. Almost all nuclei also contain a *nucleolus,* a small, dense, rounded mass of material, the function of which is not clearly understood.

Chemically, the nucleus is much like the rest of the protoplasm except that it contains a large amount of a characteristic protein called *nuclein,* of which phosphorus is an important constituent.

A cell usually contains a single nucleus, but in certain cells, known as *coenocytes*, there may be many nuclei. Indeed, among some of the algae and fungi the entire plant body is a single filament, often long and much branched, which is quite without partitions, thus seeming to be a single huge cell provided with hundreds of nuclei. Such forms demonstrate that the ordinary activities of a plant may be carried out perfectly well in the entire absence of the usual cellular organization.

The Cytoplasm.—The remainder of the living material of the cell is known collectively as the cytoplasm, and in a typical mature plant cell is disposed in a rather thin layer just inside the cell wall and immediately surrounding the sap cavity (Fig. 12, C).

In the cytoplasm are carried out the various activities of the cell under the control of the nucleus. Some of these seem to be performed by the cytoplasm as a whole, but others are associated with definite bodies of various sorts, notably the *plastids* (Fig. 12, *P*). Important among these are the *chloroplasts*, usually small roundish bodies present in the cells of the green tissue of leaves and in certain other parts of the plant exposed to light. These contain chlorophyll, through the activity of which organic food is manufactured. *Chromoplasts*, which are related closely to chloroplasts and derived from them but which contain other pigments, are responsible for many of the red and yellow colors of plants. *Leucoplasts* are colorless plastids, some of which serve as centers for the deposition of starch grains in storage tissues.

In addition to the plastids there are usually other bodies in the cytoplasm which are very minute and appear as tiny granules, rods, or threads, the nature and functions of which are not well understood. They are called *chondriosomes* or *mitochondria*. It has been suggested that they are the bodies from which plastids develop, that they are concerned with respiration, or that they are merely food substances.

On the outside of the cytoplasm (next the wall) and on the inside (next the vacuole) is developed a delicate *plasma membrane*, through which must pass everything that enters or leaves the cytoplasm. This functions as an osmotic membrane, and thus controls the entrance and exit of water. It is noteworthy that these membranes are permeable to certain dissolved substances but are impermeable to others, and that this permeability varies in different tissues and under different conditions. The character of the plasma membranes is thus of the utmost signifi-

cance to the plant, since they control the interchange of all material between the cell and its environment.

The Vacuole.—In animal cells and in young plant cells the nucleus and cytoplasm fill most of the cell, but in typical mature plant cells the central portion is occupied by a droplet of liquid, the *vacuole,* or *sap cavity* (Fig. 12, *V*). This usually originates from the fusion of a number of smaller vacuoles which are present in the embryonic cell. The water within the sap cavity, or *cell sap,* contains various substances in solution, notable among which are sugars and organic acids of various types. Pigments are often present here, and most of the red and blue colors in plants are sap colors.

Water and dissolved substances enter the sap cavity by diffusion through the cytoplasmic membranes, and the concentration of the sap solution is an important factor in determining the rate of this diffusion, and in maintaining the cell in a plump and well-filled condition.

The Cell Wall.—Surrounding the cell is a wall of varying thickness which is laid down as a secretion on the outside of the cytoplasm (Fig. 12, *B* and *C*). It is probably quite inert and dead, and serves merely as a skeletal framework to support the softer parts of the cell. The first-formed or *primary* wall, produced while the cell is very young, is composed largely of a jelly-like material, pectose, which later becomes the *middle lamella* or cementing substance. Inside this is produced later the *secondary* or main wall of the cell, composed largely of cellulose. In certain types of tissue, such as wood, this wall may become very hard and firm, or *lignified,* by its conversion into ligno-cellulose. In corky tissue the wall is infiltrated with a fatty or waxy material which renders it impermeable to water. Wherever these changes tend to prevent the free passage of water through the wall, there are thin areas or *pits* in it where the secondary wall fails to develop and only the thin primary one is present (Fig. 13). In certain types of wood cells these pits are very complex in character, and are known as *bordered pits.*

Various Types of Cells.—Cells which perform the same function are aggregated into tissues, and become modified variously in size, shape, and structure. In the simplest type of tissue, such as that used for storage, the cells are roughly spherical and rather thin walled; in many water-conducting tissues they are thick walled, much elongated parallel to the stem axis, and soon lose

their protoplasmic contents; in the food-conducting tissues of the phloem the cells are somewhat elongated and the end walls are perforated, so that there are direct protoplasmic connections between one cell and the next; in certain kinds of skeletal tissue the walls become so very thick that they fill almost the entire cell cavity; in the so-called *latex* tissues, by which milky sap is produced, the cells are exceedingly long, and penetrate the other

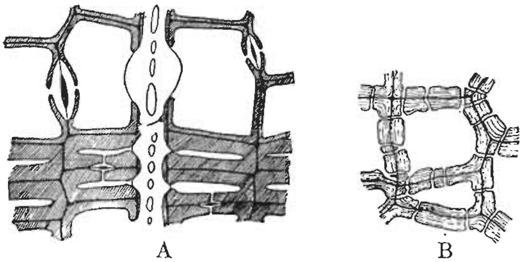


FIG. 13.—Pits in thickened cell walls. *A*, wood cells of pine, showing bordered and half-bordered pits; *B*, stone cells of sycamore, showing simple pits (*From Eames and MacDaniels.*)

plant tissues for considerable distances; and there are many other types of cellular modifications. At the growing points, such as the buds and the cambium, where new cells are being formed continually by division, the cells are very simple in construction. As the organs which develop from this growing point mature, the cells which compose these tissues become variously differentiated until a structure is produced in which all sorts of physiological activities may be going on at the same time, in specialized cells or cell aggregates. An understanding of this cellular organization of plants is essential if one is to study intelligently either the morphology or the physiology of the plant body.

QUESTIONS FOR THOUGHT AND DISCUSSION

46. Why is protoplasm regarded as the only "living" portion of the plant?

47. What significance is there in the fact that life seems always to be associated with substances which are complex chemically and unstable physically, like proteins and colloids, rather than with relatively simple and stable substances?

48. Give an example of a colloidal system in which a liquid is dispersed in a gas; a gas in a liquid; a solid in a gas; a solid in a liquid.

49. Why can so little be learned about the structure of protoplasm from a microscopic study of cells which are alive?

50. What parts of a typical cell do you regard as being really alive? Give reasons for your answer.

51. Enumerate some of the advantages of cellular structure in plants and animals.

52. Do you think that it is more logical to regard the entire plant as an *individual* divided into cells, or to regard each cell as an individual and the entire plant as a colony of cells? Give reasons for your answer.

53. Why should it be that cells are such very small objects?

54. In general, the smaller a cell is, the more active it is physiologically. Explain.

55. Most plant cells tend to assume a spherical shape if free from contact with other cells. Explain.

56. Why do so many cells have a six-sided appearance when seen in section?

57. Of what advantage is the streaming of cytoplasm which often takes place in cells?

58. In the simplest and most primitive plant cells the protoplasmic contents seems to be essentially homogeneous, but in higher types there are many kinds of specialized structures present (nucleus, plastids, chondriosomes, and others). What reasons can you suggest for this increased complexity of cellular structure?

59. What important functions does the cell wall perform?

REFERENCE PROBLEMS

18. When and by whom was the Cell Theory first formulated? When and by whom was the term *protoplasm* in its present sense first used? Who discovered that every cell has a nucleus?

19. State two fundamental differences between a typical plant cell and a typical animal cell. With what general differences between animals and plants are these cellular differences correlated?

20. Enumerate as many examples as you can of cellular structures which are useful to the plant after the cells are no longer alive.

21. What importance has been attached to the relative bulk of nucleus and cytoplasm (the nucleo-cytoplasmic ratio) in plant cells?

22. In typical undifferentiated tissue like pith, where the cells are essentially spherical in shape, how many sides (or points of contact with adjacent cells) may a cell be expected to have?

23. Outline briefly the "reticular," "filar," "granular," and "alveolar" theories as to the physical structure of protoplasm.

24. What is the difference between "mechanistic" and "vitalistic" theories as to the nature of life?

25. State briefly the doctrine of "Spontaneous Generation," and explain why it is no longer accepted by biologists.

26. What prevents the cells of a plant from separating from each other and thus causing the organism to disintegrate?

27. Describe briefly the technical processes (killing, imbedding, sectioning, staining, mounting, and so on) which must be carried out in the preparation of most plant structures for microscopical study.

28. Give the author and title of three important books on cytology, and outline briefly the content of each.

29. Name several botanical investigators who have done important work in cytology, and state the notable contributions made by each.

30. Give the derivation of the following terms and explain in what way each is appropriate:

Protoplasm	Vacuole	Chloroplast
Cytoplasm	Colloid	Chondriosome
Nucleus	Chromosome	Coenocyte

CHAPTER IV

THE ROOT AND ITS FUNCTIONS

A plant, like every living organism, is built up of cells, often many millions or even billions of them. These are grouped into the particular tissues and organs in which the various activities of the plant are carried out, and a complex and highly organized individual results. This plant body as a whole is divided into two major portions, sharply distinct from each other in structure and in function. These are the *root* system, situated in

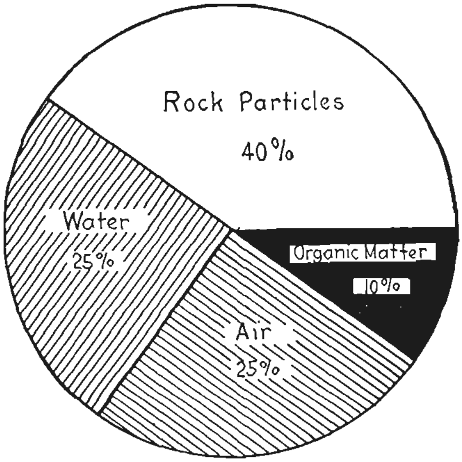


FIG 14.—Composition of soil. Graph showing the various constituents, by volume, of a rich, loam soil.

the soil where it anchors the plant and from which it absorbs water and mineral nutrients; and the *shoot* system, comprising the leaves and their supporting stems, situated in the air and concerned with the manufacture of organic food from raw materials brought up from the soil and drawn out of the atmosphere. A study of the plant, therefore, so far as its vegetative structures are concerned, naturally falls into two main subdivisions, one concerned with the root and the other with the leaf and stem.

It is perhaps more profitable to begin with a consideration of the root system.

No part of the plant can be studied intelligently without an understanding of the particular environment in which it lives and this is especially true in the case of the root. The medium in which this organ grows—the soil—is exceedingly complex physically, chemically, and biologically, and exerts a profound influence on the life of the plant. Before the structure or functions of the root system are described in detail, it will therefore be useful to discuss briefly the soil and its various constituents.

THE SOIL

The soil has three main uses in the plant's economy: it provides an anchorage and support whereby the plant may be held firmly in position; it furnishes the supply of water which the plant uses; and it contributes certain mineral salts essential to the plant's successful activity.

Soils vary much in physical texture, chemical composition, depth, origin, richness, and other respects, but all normally are made up of a mixture of distinct components, each of which has its particular influence upon the life of plants. These components are rock particles, water, air, organic matter, dissolved substances, and organisms (Fig. 14).

Rock Particles.—The bulk and the basic material of a soil is composed of small, angular particles which have been formed by disintegration of rock. These make up 90 per cent of the weight of ordinary good soil, furnish the necessary anchorage for the plant, and, through the substances dissolved from their surfaces, contribute to the supply of available nutrient materials. The particles vary greatly in size, from those of fine clay to those of coarse gravel. They differ also in shape and in chemical composition according to the type of rock producing them. The irregularity of contour which these particles display makes it impossible for them to fit very closely together, and a considerable amount of space (*pore space*) is thus left between them which may be occupied by air or by water. In soils which are in good condition for the growth of ordinary plants the particles cohere in groups to form *crumbs* or *floccules* (Fig. 15), the component grains of which are held together by water films or by such a cementing substance

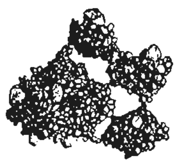


Fig. 15.—Soil crumbs or floccules, much enlarged.

as clay. One important purpose of tillage is to impart this crumb structure or *flocculation* to a soil. At the soil surface, by the direct action of the rain or by other means, these crumbs may be broken into their constituent particles, which then pack closely together and on drying harden into a firm, clay-like crust.

Water.—Water is of vital importance to plants in many ways. It constitutes the great bulk of their bodily material; it enters into the manufacture of food; it assists in maintaining the plumpness and rigidity of the tissues; and, in its capacity as a

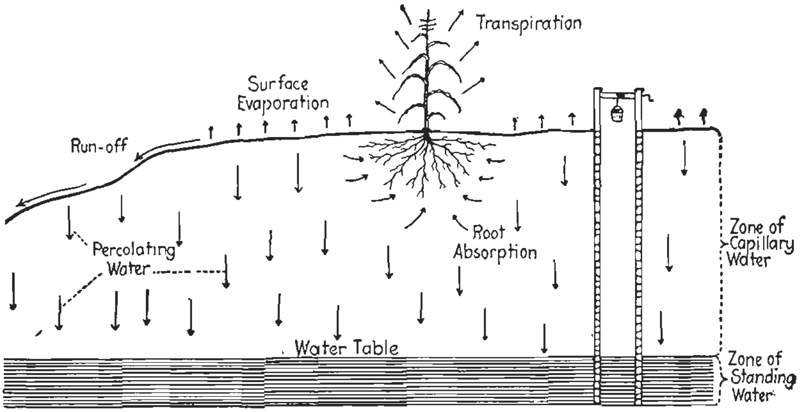


FIG. 16.—The various fates of rain water which falls upon the soil. It may run off without entering the soil; it may be evaporated from the surface; it may enter plant roots and be transpired from the leaves; it may be held in the soil by capillarity; or it may percolate downward to the water table.

solvent, it serves as the general medium in which most physiological processes are carried on.

The chief source of soil water, and in most cases the only one, is the rain which falls upon the soil surface. Various fates await this water (Fig. 16). A considerable part of it may not enter the soil at all if the surface is hard or the rainfall heavy, but may drain away instead. This *run-off* is lost to plants, and may even do much harm by washing away a portion of the soil itself. The water which does enter the soil either may *percolate* downward between the particles under the influence of gravity, or may be held in the soil by *capillarity*.

Percolating or *gravitational* water passes downward rapidly if the soil particles are coarse, more slowly if they are finer, until it arrives at a level where all the soil spaces are filled with standing or *hydrostatic* water. This level is known as the *water table*. Its

position at any given point determines the height at which water will stand in a well dug at that point, and its distance below the surface varies from place to place and is subject to much fluctuation. A similar saturated condition occurs in the upper soil layers after heavy rains, but persists there only for a short time. When water has percolated downward to this level it often is beyond the reach of roots, and is thus quite unavailable to plants.

Capillary water is water held in the soil by the force of capillarity. Common observation teaches that when an object (such as one's hand) is immersed in water and then lifted out again, some water still adheres to its surface in a thin film, or "wets"

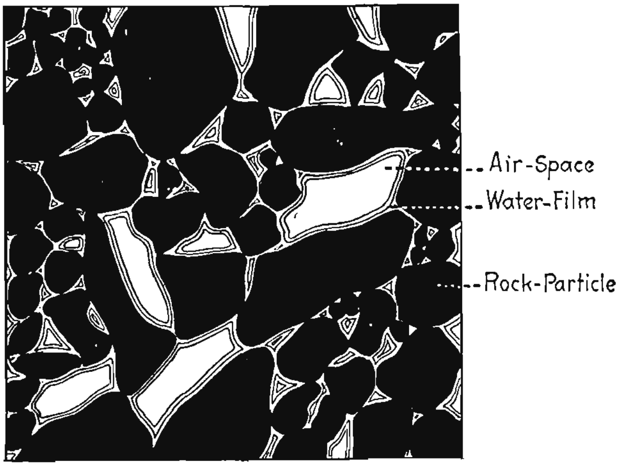


Fig. 17.—Section through soil, much enlarged. A capillary water-film surrounds each particle and fills the narrow spaces between particles. The larger spaces are occupied by air.

the object. This is due to the fact that there is greater attraction between the surface of the object and the water than is exerted by the force of gravity or the cohesion of the water particles themselves. Any material with a large amount of surface, internal or external, which may be wetted (such as a sponge, blotting paper, or coarse fabric) will therefore hold within itself, when thoroughly soaked, a great amount of water which will not drain out under gravity. For exactly the same reason, much of the water entering a soil will fail to percolate through it but instead will adhere in thin films to the surfaces, very great in total area, which are presented by the multitude of soil particles. If the amount of rainfall is small, all of it may thus be retained and none lost through percolation. Each particle in such a

moist soil is covered by a thin layer of water (Fig. 17). The films about adjacent particles coalesce, filling the minuter spaces and lining those that are larger, and a continuous film system is thus set up. It is this *film* or *capillary* water which furnishes plants with the great bulk of their water supply. One of the important objects in manipulating a soil is to increase, by one means or other, its *water-holding capacity*, and thus to prevent waste through run-off or percolation.

The principle of capillarity is of further importance in determining all movements of water in the soil other than the downward one due to gravity. The familiar fact that when a narrow glass tube is placed in water, the water will rise inside the tube to a point somewhat higher than its level outside, is due to the attraction between the surface of the glass and the water, an attraction which is sufficient to lift water against gravity. The lifting force will be proportional to the exposed surface of the tube, and therefore where the volume of water is small in relation to this surface (as is the case inside the tube) the water will rise somewhat before the weight of the lifted column counterbalances the pull exerted by the surface attraction. Obviously, the narrower the tube, the higher the column of water will rise, since the volume of liquid to be lifted will be smaller in proportion to the area of the attracting surface. Thus, in any material the structure of which presents a great amount of surface surrounding small but communicating tubes, pores, or other narrow spaces, as in blotting paper, lamp wicks, and the like, water evidently will be carried to a considerable distance in all directions by capillarity. Just such a material as this is the soil. The multitude of its tiny particles, packed closely together, form a capillary system which is able to carry water far. This water tends to surround each particle in a thin, capillary film, but if the soil particles are very coarse the film cannot pass around them and under such conditions the ascent of water necessarily stops. Water moves readily within the films and when those at the top of the ascending column are thinned, through evaporation or through the attraction exerted by still higher and unwetted surfaces, the films below are drawn upon, and water passes upward through the whole system. This movement continues until the weight of the water lifted balances the surface attraction at the top of the column. The height to which water will rise by capillarity is dependent chiefly on the size of the soil particles;

for the smaller the particles, the larger will be their surface in proportion to the spaces between them, and thus the higher will be the rise of water (Fig. 18). In ordinary soil this rise varies roughly from two to six feet. It is evident, therefore, that water which has percolated very far below the surface ordinarily cannot be made available to plants again through capillary ascent.

In most soils there is a capillary movement of water toward the soil surface, where it evaporates. If the particles at the

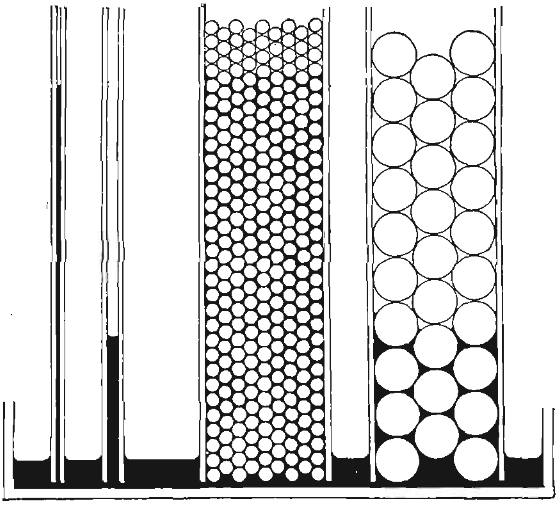


FIG. 18.—Rise of water by capillarity. In the two glass tubes at the left, the rise of water is much higher in the narrower than in the wider one. In the two chambers at the right, which are filled with spheres, the rise of water is much higher where the spheres are smaller.

surface are very close together, as they are where the soil has been packed down or where a crust has been formed, a very efficient capillary system is produced there which connects the soil surface with the deeper water-holding layers, and thus greatly hastens the loss of water by drawing it up to a point where it may be evaporated (Fig. 19). An important purpose of tillage is to prevent such waste of water by breaking up the capillary system at the surface and forming there a layer of loose, coarse material called a *mulch*.

Capillary movement of water is by no means always vertical, but may take place in all directions within a soil, just as ink spreads in all directions in a piece of blotting paper. This move-

ment tends to continue until the water films are of equal thickness throughout the entire soil mass, causing it to be uniformly moist. When water is removed at any particular point, as by surface evaporation or root absorption, it is therefore drawn thither from all other points until equilibrium is restored.

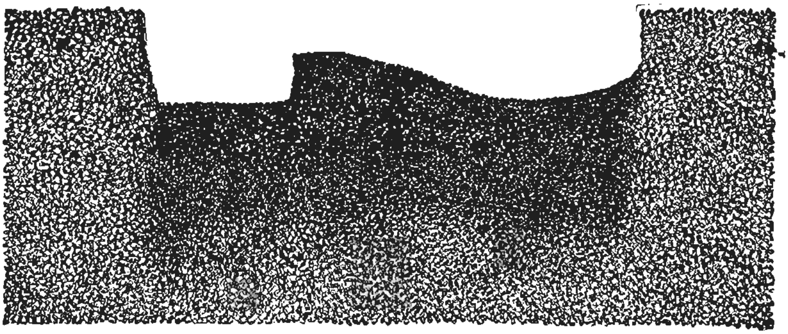


FIG. 19.—A foot-print in loose soil. A vertical slice cut through the soil under and near a foot-print, showing how the particles have been pressed together. This establishes a better capillary connection with the lower soil layers and causes more rapid movement of water to the surface, thus making the foot-print moist while the soil surface around it is dry.

In soils which have lost all their capillary water by evaporation, there still remains around each particle an exceedingly thin layer of *hygroscopic* water, which clings so tenaciously that it may be driven off only by subjecting the soil to a high temperature. When the air is very dry this water is present in minimum amount, but when humidity rises, more water may be taken up directly from the air, or *hygroscopically*. This type of water is removed with such difficulty from the soil particles, however, that the plant is able to obtain little or none of it.

Air.—Since oxygen is essential for the healthy growth of ordinary plant roots, the presence in the soil of a plentiful supply of air is a matter of vital importance. If the spaces between the soil particles become filled with water, most of the air is necessarily driven out, and when this condition of saturation is long maintained, ordinary plants suffer. Such excess of water, however, normally passes downward by percolation, and as it does so the soil spaces again fill with air. In most cultivated soils, from 20 to 35 per cent of the volume consists of air spaces. Plowing tends to increase greatly the air content of a soil, since the structure of the whole mass is loosened and the crumbs are more widely

separated. A soil in this condition is said to be in good *tilth*. Where water occurs only in capillary form much air is present in the larger spaces, and such a state of the soil is therefore clearly the most favorable for plant growth since then, and then only, is a plentiful supply of water combined with a plentiful supply of oxygen.

Organic Matter.—All rich soils contain a considerable amount of material derived from the dead bodies of organisms, particularly of plants. Roots which die and remain in the soil, and leaves and other plant parts which fall on the soil surface, are the sources from which this organic matter is mainly derived in nature. In the practice of agriculture it is increased in amount by manuring and other artificial means. After entering the soil it soon begins to undergo decomposition, and for the most part is broken down finally into simple end-products—carbon dioxide, water, and ammonia. As this organic material decays it becomes characteristically dark in color and undergoes a series of complex chemical changes, in which condition it is known as *humus*.

Organic matter is of importance to plants in many ways. It improves the physical condition of the soil, for because of its coarse and fragmentary character it tends to separate the particles and thus to increase materially the air content of the soil. Since organic matter absorbs water readily, its presence also adds to a soil's water-holding capacity. The decomposition of humus liberates certain nutrient materials, notably an abundant supply of nitrogen compounds, which ultimately become available to plants. Organic matter is also the seat and food supply of the soil bacteria, minute organisms which are indispensable in plant nutrition. Any treatment of the soil which will increase its humus content will therefore tend to increase its productivity, and whatever decreases the humus content will impoverish the soil.

Dissolved Substances.—Soil water is by no means pure water, but carries dissolved within it a great variety of substances. Anything which is to be taken in by the roots of plants must be in solution, and therefore these dissolved substances are the only portion of the soil, aside from water itself, which is directly available as nutrient material for plants. Their origin and chemical composition are consequently of much botanical importance.

The solvent power of soil water is increased by the presence within it of carbon dioxide, liberated in the respiration of plant

roots and of the lower organisms. Thus reinforced, water not only attacks the surfaces of the rock particles but absorbs any soluble material which may appear in the humus or as a product of bacterial activity.

A great variety of substances are present in the soil solution, and chemical analyses of the ash* of plants show that very many of these may be taken into the plant body. Compounds of nitrogen, sodium, potassium, calcium, magnesium, iron, manganese, aluminum, phosphorus, sulphur, chlorine, and silicon are commonly absorbed by the roots, and many others may be taken up in smaller quantities. Certain of these elements are far more important to the plant than others, however, and it has been clearly proven by experiment that seven—nitrogen, sulphur, phosphorus, calcium, magnesium, potassium, and iron—are essential for normal plant growth. Recent investigation has also shown that exceedingly minute amounts of a number of others, among them boron, manganese, and zinc, are also necessary. The actual bulk of these various mineral nutrients taken up by the plant is very small in proportion to the size of the plant body, but in the activities of protoplasm each plays a necessary part, and a soil which is deficient in any one of them will be unable to support vegetation successfully.

The removal of large amounts of nutrient materials from agricultural soils, in the form of crops and in other ways, reduces the available supply of certain chemical elements (notably nitrogen, phosphorus, and potassium) to such an extent that a fresh supply must be returned to the soil if abundant plant growth is to be maintained permanently thereon. This necessitates the common practice of adding to the soil various types of fertilizers which renew the supply of essential salts there available to plants.

Organisms.—Aside from its service as a medium for the root growth of higher plants, the soil provides a dwelling place for a great variety of other organisms, the activities of which have a profound effect on the composition of the soil and on the processes occurring therein. Rodents, insects, and angle-worms all modify the physical character of the soil by their abode there. Those most minute and lowly of living things, however, which are grouped together as *micro-organisms* are of far greater impor-

* The *ash* of plants is the residue left after complete combustion of the plant tissues, and an analysis of it indicates the amount and character of mineral substances present in the plant.

sance, for experiment has shown that without their presence the toil would soon become unfit to support a vegetation of higher plants.

Most notable among these micro-organisms are the bacteria (Fig. 20), tiny, single-celled plants which lack chlorophyll. Many of these—the bacteria of decay—decompose the complex organic substances found in humus into such simple end-products as carbon dioxide, water, and ammonia, thus releasing great quantities of nutrient materials which would otherwise be locked

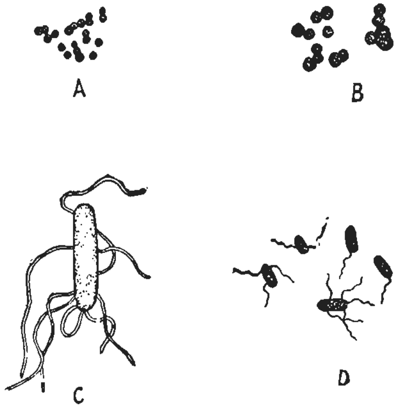


FIG. 20.—Some important soil bacteria. *A*, nitrite bacteria, *Nitromonas*. × 2000; *B*, nitrate bacteria, *Nitrobacter*. × 2000; *C*, a common decay-producing organism, *Bacterium mycoides*. × 1500; *D*, nitrogen-fixing bacteria, *Rhizobium leguminosarum*. × 750.

up and useless in the dead bodies of animals and plants. Still other bacteria in the soil effect chemical change of various sorts, the results of which are of great moment to the higher plants. Especially important are bacteria concerned with the transformations of nitrogen and its compounds, for through their activity the available supply of this necessary element is maintained in the soil.

The continual circulation of nitrogen through its various successive stations in organisms, air, and soil, is known as the *nitrogen cycle* (Fig. 21). Complex nitrogenous substances returned to the soil in the bodies of dead animals and plants are broken down by the bacteria of decay into simpler compounds, which are finally reduced to ammonia. Since most plants can use nitrogen only when it occurs in the form of nitrate salts, however, this ammonia is not available directly to them but must

first be converted into such salts through the process of *nitrification*. This is carried on by two types of *nitrifying* bacteria; the nitrite bacteria, which change ammonia to nitrites, and the nitrate bacteria, which in turn convert nitrites into nitrates. In this form nitrogen is readily absorbed and assimilated by plants, and ultimately is returned to the soil again through the bodies of plants or animals, thus completing the cycle.

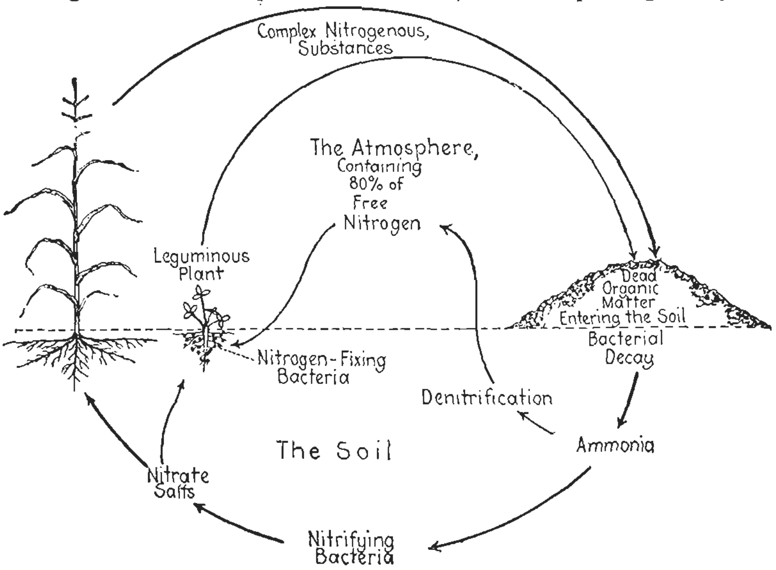


FIG. 21.—The nitrogen cycle.

Through the activity of another group of these minute organisms, certain of the seed plants are also able to take advantage of the enormous supply of nitrogen in the atmosphere, which ordinarily is quite unavailable. These are the *nitrogen-fixing* bacteria. They are present in most soils and cause the development of the tubercles or nodules usually found on the roots of plants belonging to the Legume family (Fig. 22) which includes the bean, pea, clover, alfalfa, and their allies. These bacteria are able to absorb the free gaseous nitrogen of the air and to build it into nitrogenous compounds in their bodies, whence it ultimately becomes available to the particular plant on the roots of which the bacteria grow. Without drawing at all upon the nitrogen compounds in the soil, a leguminous plant is consequently able to acquire an abundant supply of this important element. Certain other

bacterial types, notably species of the genera *Azotobacter* and *Clostridium*, which live freely in the soil and are not associated with any other plant, are also able to absorb gaseous nitrogen and to build it into complex organic substances; and these micro-

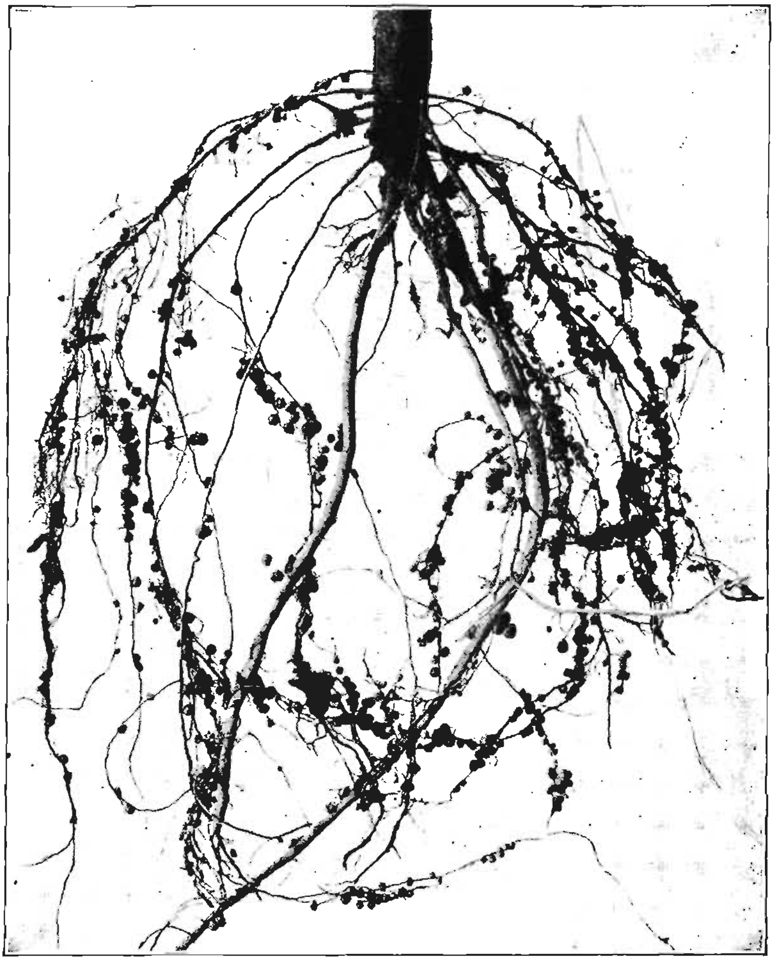


FIG. 22.—Root system of a soy-bean plant, showing the root tubercles produced by nitrogen-fixing bacteria. (*From Piper and Morse.*)

organisms are often of considerable importance in increasing the supply of available nitrogen in the soil.

In the case of many species of plants, particularly those which grow in forests or other situations rich in humus, thread-like

filaments of fungi are intimately associated with the smaller roots, entering their outer tissues and surrounding the root with a web-like jacket of fungus threads. These often largely take the place of root hairs and aid the plant in absorbing water and nutrient material from the soil; and the fungus seems also to benefit by such relationship. This root-fungus association is known as a *mycorhiza* (Fig. 23). Certain plants have become so dependent in this way upon particular species of fungi that they cannot thrive when the latter are absent.

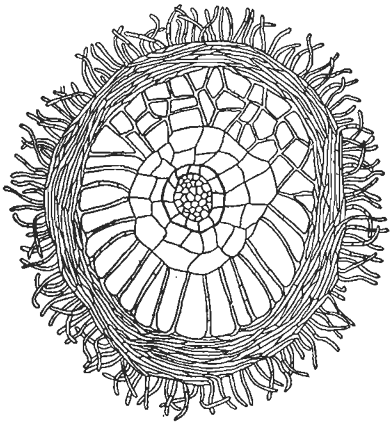


FIG. 23.—Cross section of a young root of hickory, showing the mycorhizal fungi surrounding it and entering its outer tissues. (*From McDougall.*)

The extreme complexity of the soil and the vital significance to plants of its composition and of the changes which go on within it should be clearly recognized. The study of this remarkable material has required the collaboration of almost all of the sciences, but a precise knowledge of many of its aspects is still lacking and the various ways in which it affects the life of plants growing in it are not all fully understood.

THE ROOT

The portion of the plant most intimately related to the soil is the root. This organ has two major functions—to anchor the plant firmly, and to absorb water and certain important nutrient materials from the soil. Beyond this, the root often serves as a storage reservoir for food and may perform various other functions.

External Structure.—The most common type of root is a rather slender and profusely branched structure, penetrating the soil in all directions and forming a *fibrous* root system (Figs. 24 and 25). Its advantages for anchorage and absorption are obvious. Somewhat less common are types which possess a single main root or *tap root*, penetrating deeply into the soil

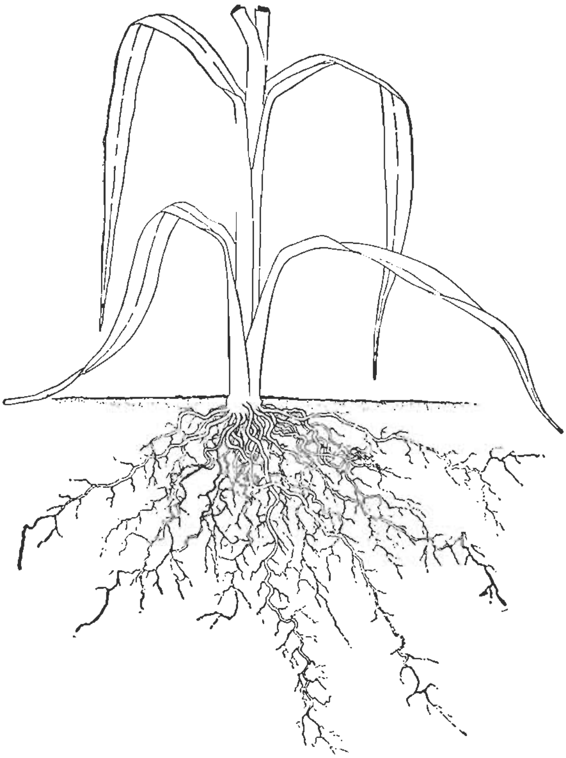


FIG. 24.—A fibrous root system (grass). The roots are all rather slender and are much branched.

and much stouter than the *lateral roots* which arise from it (Figs. 26 and 27). Tap roots lend themselves readily to storage purposes and frequently become large and fleshy. The root systems of many plants are intermediate between these two main types. Whatever is a direct continuation of the main root of the young seedling plant is known as the *primary* root, and the branches arising from this are called *secondary* roots. In some

plants the primary root long maintains its ascendancy, but in others it soon is equalled or exceeded by the numerous secondary branches.

The typical root system is subterranean and develops from the primary root of the seedling, but under certain conditions roots may also appear on other parts of the plant, particularly the stem and leaves. Such *adventitious* roots are often developed nor-

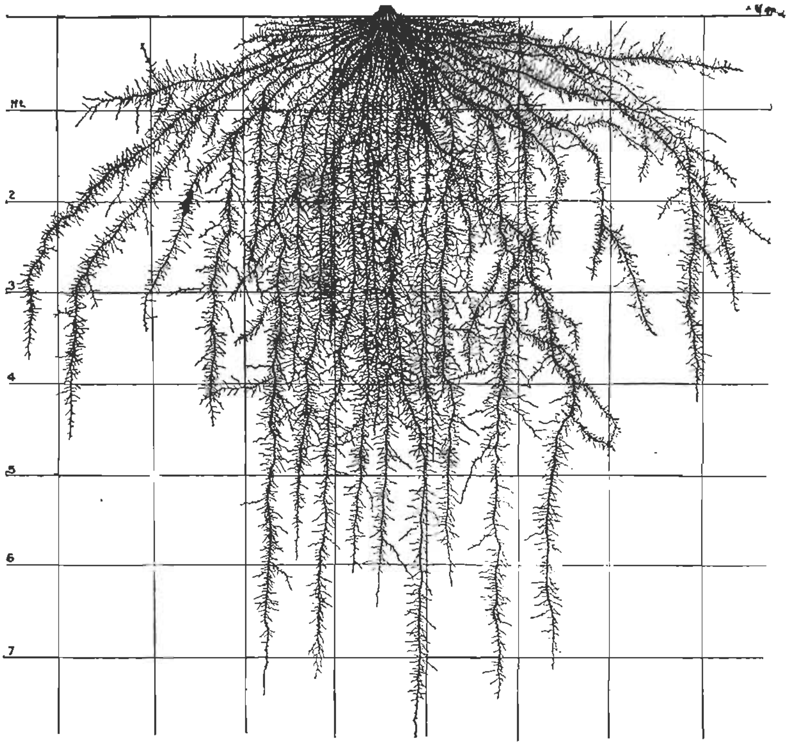


FIG. 25.—Fibrous root system of mature corn plant, showing its distribution in the soil. (*From Weaver.*)

mally, as in the case of the rootlets which hold the stems of English ivy or poison ivy firmly to a support, or those which grow out from the "runners" of a strawberry plant. These also are familiar in various methods of artificial plant propagation, for if a "cutting" (a small shoot, a piece of the stem, or sometimes even a part of a leaf) is removed and placed under favorable conditions, adventitious roots will grow out from it, and a new plant

thus becomes established. It is of interest to note that although roots thus may frequently grow from isolated stems and leaves, it is only rarely that buds, capable of producing stems and leaves, will develop on roots.

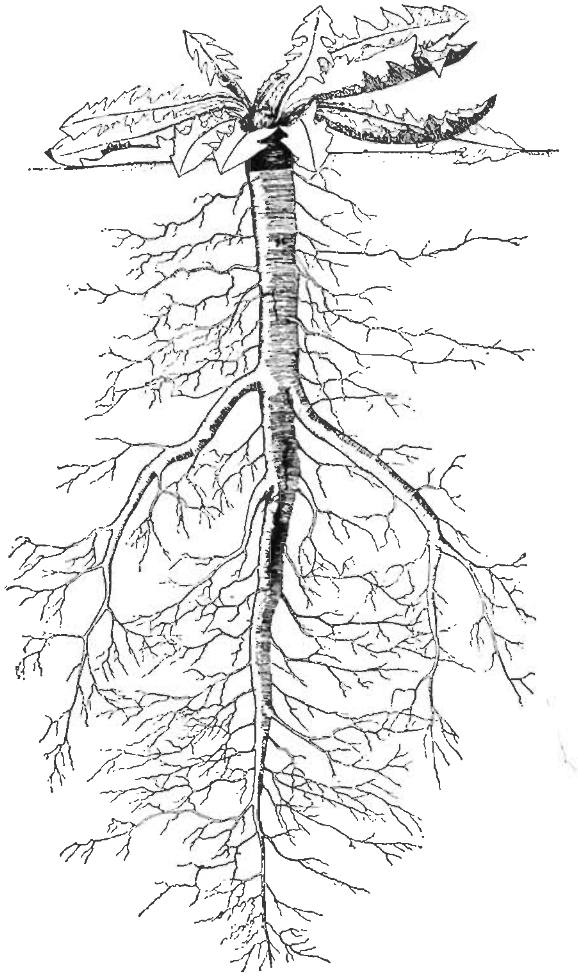


Fig. 26.—A tap-root system (dandelion), showing the main tap root and the numerous smaller lateral roots.

Various factors in the soil, notably water, mineral nutrients, and oxygen, markedly affect the extent and the character of root growth (Fig. 28). Even under similar conditions, however,

two different species may have root systems which are as different in size, shape, and character as are the above-ground portions of the plant. Some are very deep rooted, occasionally penetrating twenty feet or more into the soil, while others have shallow roots which develop close to the soil surface. Some plants have large roots and others relatively small ones. Some have a much-

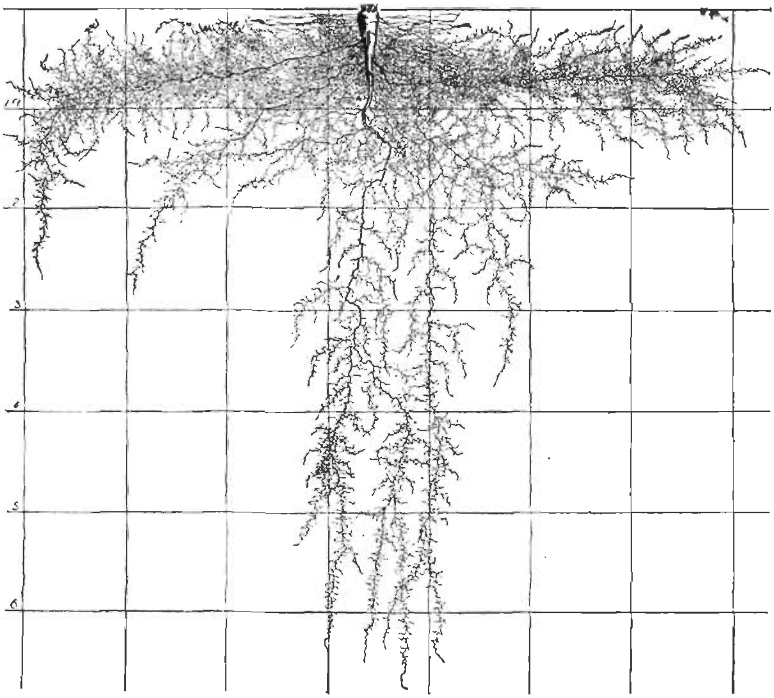


FIG. 27.—Tap-root system of mature parsnip plant, showing its distribution in the soil. (*From Weaver and Bruner.*)

branched system, filling the soil in all directions with their delicate strands, while others have fewer but stouter branches. Various species also differ markedly in the response of their roots to environmental conditions.

The Absorbing Region.—Absorption of water and nutrient material is carried on only by the younger portions of a root, near its tip. The very tip itself is usually covered with a sheathing *root cap* of cells, which protects the delicate underlying tissues as the root pushes its way through the soil (Fig. 29, *A*). Back of

this is a short region of growth, the only place where elongation of the root occurs (Fig. 29, *B*). Behind this, in turn, is the absorbing region, a somewhat longer zone, the surface of which is covered with thousands of exceedingly delicate filaments, the *root hairs* (Fig. 29, *C*). Each hair is an elongated projection growing out

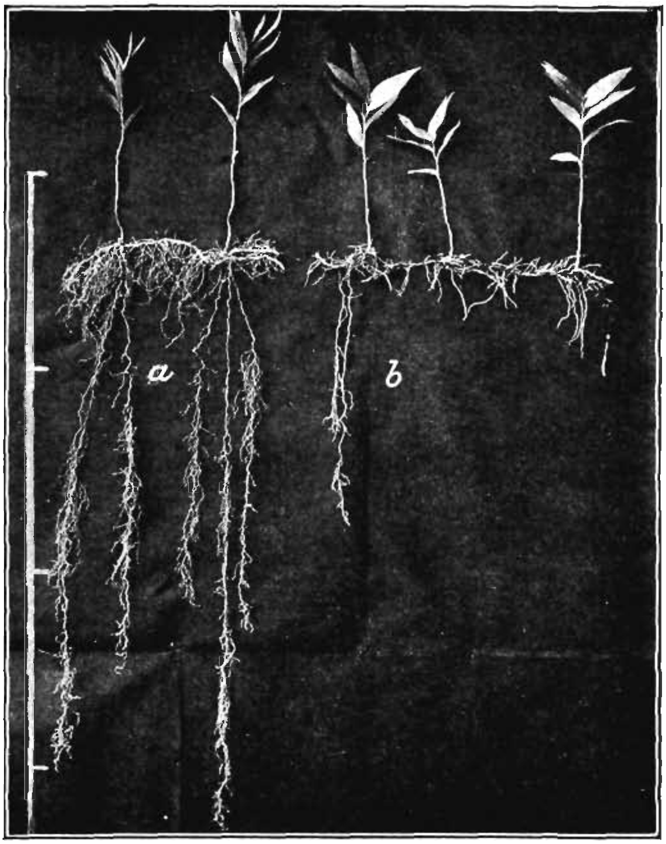


FIG. 28.—Root systems of plants of false Solomon's seal growing under different conditions: *a*, in dry gravelly soil; *b*, in moist soil in the shade of the forest. Scale at left in feet. (*From Weaver.*)

from one of the surface cells of the root (Fig. 30), its vacuole and lining of cytoplasm being continuous with those of the root cell of which it forms a part (Fig. 31). The root hair may reach a length of several millimeters, and forces its way into the minute crevices of the soil, thus coming into most intimate contact with

the soil particles (Fig. 32). Through the very extensive surface which these root hairs expose to the soil, absorption of water and mineral salts takes place. Root hairs generally are short-lived, dying away as the corky bark begins to appear. A root-hair zone of fairly constant length thus follows behind the growing root tip, new hairs appearing in its younger portion to replace the oldest ones, which are continually dying away. The absorption of

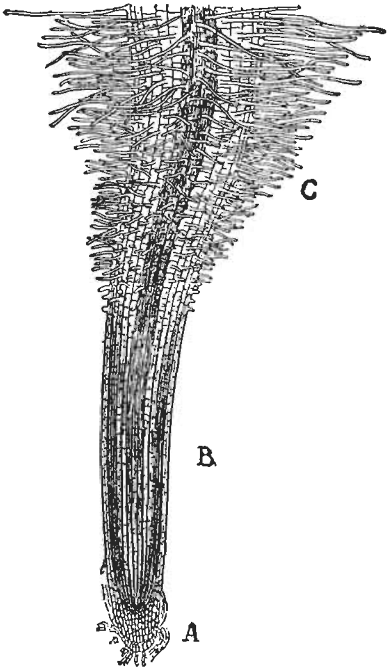


FIG. 29.—Tip of a root showing root cap (*A*), growth zone (*B*), and root-hair zone (*C*). (*From Ganong, "Textbook of Botany," copyright by the Macmillan Company. Reprinted by permission.*)

material from the soil is therefore carried on only by a very small portion of the root system, close to the growing tips of the young roots, and never takes place anywhere in the older portions.

Internal Structure of Roots.—Internally, roots show a marked structural differentiation. In a young root, three main cell systems or tissues are distinguishable—the *epidermis*, the *cortex*, and the *fibro-vascular* cylinder (Fig. 33).

The epidermis of the root, like that of other plant organs, is a single layer of cells in thickness. These cells normally are pro-

tective in function, but in the root-hair zone many of them produce on their outer surface a characteristic projection, the root hair itself.

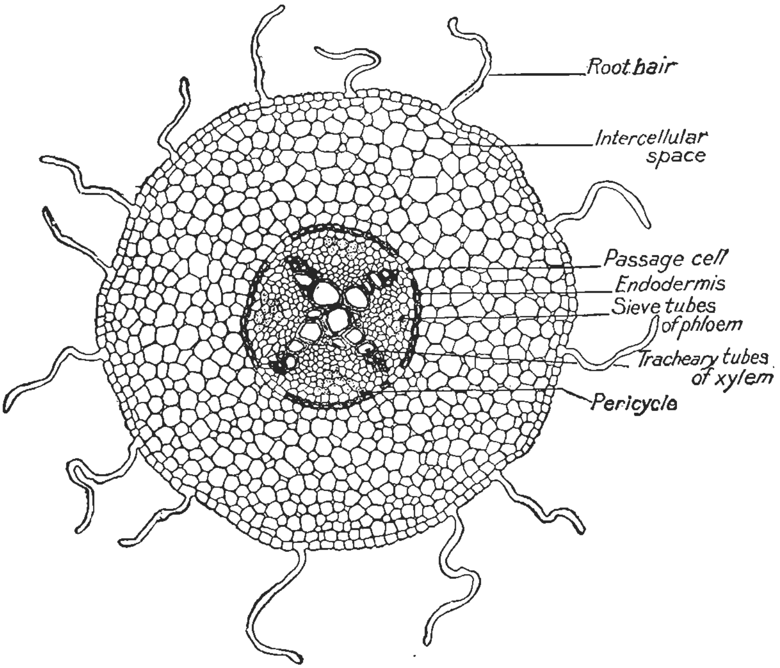


FIG. 30.—Diagrammatic section of a young root cut through the root-hair zone. (*From Weaver.*)

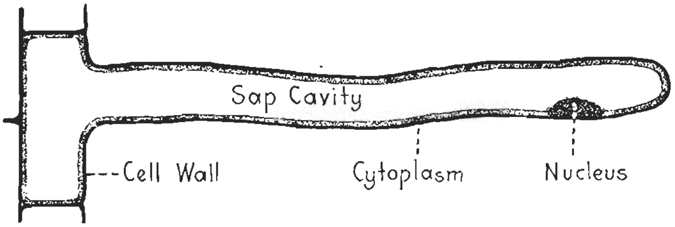


FIG. 31.—Diagrammatic section through a typical root hair, showing its various structures and its relation to the surface cells of the root.

The cortex lies just under the epidermis, and consists for the most part of thin-walled, rounded cells. In the young root these serve to transmit water and dissolved substances from the root hair to the conductive tissues in the center. Later, the cortex is

chiefly a storage region for reserve food, and in old roots it has often disappeared entirely. The innermost layer of cortical cells,

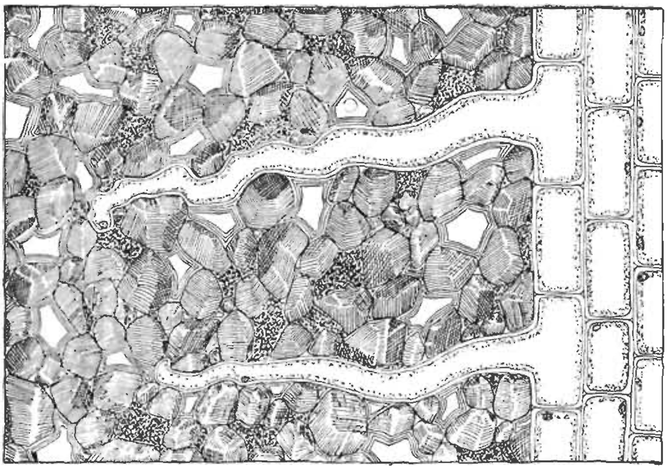


FIG. 32.—Diagrammatic section through a portion of a young root and the adjacent soil, showing two root hairs forcing their way between the soil particles. Rock particles, water films, and air spaces are indicated. Much enlarged.

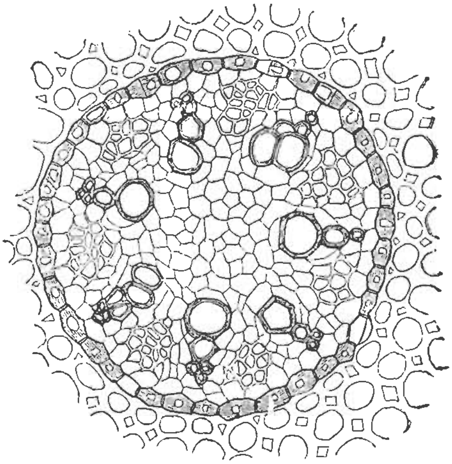


FIG. 33.—Transverse section of the fibro-vascular cylinder of a young root. The bundles of thick-walled wood cells alternate with bundles of thin-walled phloem cells. The whole is surrounded by an endodermis, composed of a single layer of thick-walled cells. Outside the whole is the cortex of the root. Note the similarities and differences between this fibrovascular system and the one shown in Fig. 30. (*From De Bary.*)

the *endodermis,* has characteristically thickened cell walls and is thought to serve in preventing the outward diffusion of food

which passes down the vascular cylinder to the growing regions of the root below.

The fibro-vascular system occupies the core of the root, furnishing mechanical strength and serving as a highway for conduction. As in the stem, it is composed of two main tissues, the wood or *xylem*, and the *phloem* (or "bast"). The wood, which forms the central axis of this cylinder, is usually star shaped in cross section and is composed chiefly of cells which are dead and possess thick and woody walls. Most of these cells are much elongated. The smaller and thicker-walled elements of the wood serve chiefly for mechanical support, but through the larger ones are carried upward the water and dissolved salts which enter the root from the soil. Between the points of the star are strands of phloem, the characteristic cells of which are the *sieve tubes*,—thin, elongated cells connected with each other by perforations in their end walls. Downward through these sieve tubes passes food manufactured in the leaves and destined for the nourishment of the root system. A more detailed account of the structure and activities of wood and phloem in plant organs will be presented in a later chapter.

In older roots the fibro-vascular cylinder, particularly as to its woody portion, increases greatly in thickness through the activity of a growing zone, the *cambium*, just as does the stem; and on the outside of the root is developed a corky bark.

Roots usually branch profusely. Each branch originates in the outer layer of the fibro-vascular cylinder as a small swelling which elongates, forces its way through the cortex, and finally ruptures the epidermis and projects from the surface of the root (Fig. 83). This method of branching is quite different from that of a stem, where a new branch develops from a *bud* at the surface.

Diffusion and Osmosis.—The most important function of the root is to absorb from the soil the water and mineral substances used in the plant's life and growth. This involves the physical processes of *diffusion* and *osmosis*, a consideration of which is necessary before this primary activity of the root can be clearly understood.

Diffusion.—Diffusion may be defined as the tendency of any substance, when it occurs as a gas or in solution, *to become evenly distributed throughout the whole space available to it by moving from points of greater to points of lesser concentration.* Its operation is familiar in the diffusion of odors, for the minute particles given

off by any strongly scented substance will move outward rapidly, even in perfectly still air, and will soon become equally distinguishable in all directions from their point of origin. Two gases liberated within a closed space soon diffuse throughout its whole extent and become thoroughly mixed. In the same way, the molecules from a crystal of salt dissolved in a vessel of water will in time become dispersed so uniformly, even though the liquid is free from moving currents, that samples taken from any

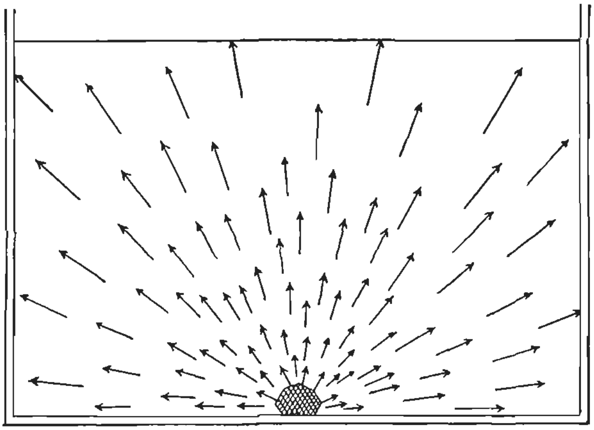


FIG. 34.—Diffusion of a dissolved substance. Diagram representing the outward diffusion of molecules which are being dissolved from the surface of a soluble substance immersed in water.

part of the contents of the vessel will be salt solutions of the same strength (Fig. 34). This constant tendency toward diffusion is explained by the fact that in gases and liquids the molecules are in very active movement, continually striking against one another and rebounding. There obviously are fewest collisions, and thus most frequent opportunity for unobstructed movement, in those directions where there are fewest molecules, and in such directions a dispersal of the molecules therefore necessarily takes place until they are present everywhere in uniform abundance. The principle of diffusion is operative in so many of the physiological processes of plants that it must be thoroughly grasped if these processes are to be understood.

When two liquids are separated by a membrane through which they can pass, diffusion between them will still take place. Such diffusion through a membrane is called *osmosis*, and it tends to continue (if the permeability of the membrane allows) until the

composition of the liquids on both sides of the membrane is the same. If a solution of salt in water, for example, is present on one side and pure water on the other, the salt will tend to diffuse through the membrane into the water, and the water into the salt solution, until the concentration is the same on both sides of the membrane. It is important to note that the *concentration* (the number of dissolved particles per unit of volume) rather than the total amount of the substance or the bulk of the solution, is the factor which determines the direction and rate of diffusion. It is by diffusion through the cytoplasmic membranes of the root hair that water and mineral salts in the soil solution enter the plant.

The Influence of the Membrane.—Osmotic diffusion is complicated, however, by the character of the membrane. If this is equally permeable to everything, so that water and all substances dissolved in water, for example, can pass through it without any hindrance whatever, diffusion between the liquids on the two sides of the membrane will take place just as though none were there, and equality of composition and concentration will soon be attained. If the membrane is impermeable to everything, on the other hand, obviously no diffusion can take place. If the membrane is neither completely permeable nor completely impermeable, however, but allows certain substances to diffuse through it while preventing, or at least retarding, the diffusion of others, then the attainment of equal concentration on both sides of the membrane necessarily is accomplished by an *unequal* interchange. Let us assume, for example, that a membrane is permeable to water but impermeable to dissolved sugar; and that on one side of this membrane there is a strong solution of sugar in water, and on the other side a relatively weak solution. Diffusion, as before, will now *tend* to equalize the concentration on the two sides of the membrane, but the sugar molecules, instead of passing from the solution where they are relatively abundant to the one where they are relatively scarce, will strike the membrane but fail to pass through it at all; whereas the water molecules, tending to diffuse from the region where they are relatively abundant (the weak solution) to the one where they are relatively scarce (the strong solution) will be able to do so, since they can readily pass through the membrane, and *this movement of water will continue until the concentration* (number of dissolved particles per unit of volume) *is equal on both sides.* It is evident, therefore,

that when two solutions of unequal concentration are separated by a membrane which is permeable to water (or any other solvent*) but is impermeable, or less permeable, to the dissolved substance or substances, water will pass from the less to the more concentrated solution until equilibrium is attained. This is what happens when such an experiment is tried in the physical laboratory. The more concentrated solution tends to expand and thus exerts a pressure, if confined within a closed

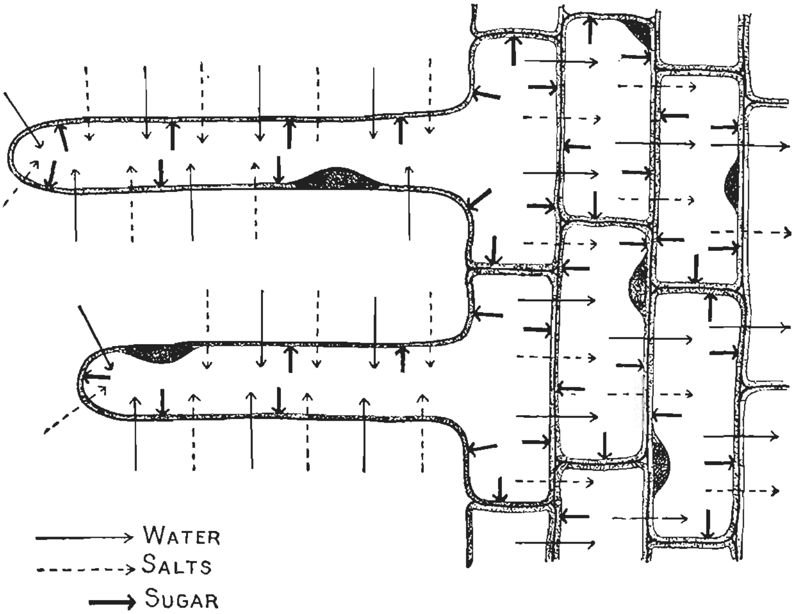


FIG. 35.—Movement of water and dissolved substances into the root. Diagram showing the entrance of water and salts into two root hairs and their passage thence through the cortical cells of the root. The cytoplasmic membranes are readily permeable to water and salts but prevent the passage of the sugar dissolved in the cell sap.

space, which may be very great. A membrane of the sort just described, which allows water to pass through it but prevents the diffusion of a dissolved substance, is called *semi-permeable*, and it is an important biological fact that the membranes in living cells are of this type.

It is exactly this principle of osmotic interchange which governs the passage of water from the soil into the root. The semi-permeable cytoplasmic membranes of the root hair readily allow

*Osmotic phenomena are shown by other solvents than water, but water, of course, is the all-important solvent in physiology.

water to diffuse through them but entirely prevent the outward passage of the sugar molecules dissolved in the cell sap. The presence of this relatively abundant supply of sugar (and similar dissolved substances), undiminished by outward diffusion, thus tends to maintain the sap solution of the root hair at a considerably higher concentration than occurs in the soil solution outside, and water therefore passes osmotically from the soil through the membranes into the sap cavity of the root hair (Fig. 35). These same membranes, however, are permeable to most of the mineral salts present in the soil, which are thus able to diffuse readily into the root hair.

Osmotic membranes, both living and dead, differ markedly in the ease with which dissolved substances of various sorts can diffuse through them. One membrane may be freely permeable to a given substance; another may allow it to pass slowly, and another may be quite impermeable to it. Nor does the same membrane affect the diffusion of all substances to an equal degree, for some may pass through it easily, others with difficulty, and still others not at all. To what these differences are due is not known, but they presumably are dependent upon the relation between the structure of the membrane and the size and character of the molecules of the dissolved substances.

Other Principles of Osmotic Action.—Before attempting to apply extensively the principles of osmosis to the living plant, however, it will be well to fix in mind certain facts with regard to osmotic phenomena about which confusion frequently arises.

First, substances which are insoluble or which for any reason are not in solution *cannot diffuse*, and have no osmotic effect whatever. Sugar, for instance, is soluble and is osmotically active, but the moment it is converted into starch, which is insoluble, it loses its osmotic effect entirely.

Second, the osmotic strength of a solution, and consequently its power to attract water, is determined not by the chemical nature of the dissolved substances but by the total concentration of material, of whatever kinds, which is in solution; in other words, by the total number of all dissolved particles* per unit of volume. A solution of sugar, one of salt, one of a mixture of the two, or one containing half a dozen different chemical substances, all may have exactly the same osmotic concentration.

*In relatively concentrated solutions these are molecules, but in weaker ones many or all of the molecules may break up into their constituent ions.

Third, the rate of diffusion of a given dissolved substance from one solution to another increases with the difference in concentration between the two solutions.

Fourth, the diffusion of water and the diffusion of a dissolved substance through the same membrane occur *quite independently of one another.* Water will move through a membrane from a solution of lesser total concentration of dissolved substance (and thus of more abundant water) to a solution of greater total concentration (less water); and substances dissolved in this water, following the same law of diffusion, will also tend to spread from where they are more abundant to where they are less so. The fact that one group of molecules is dissolved in the other group does not affect their independence of diffusion. Given the proper conditions, it is quite possible for a dissolved substance to pass through a membrane osmotically with no movement of water taking place at all, or for water to move without a movement of substances dissolved in it, or for water to pass in one direction and dissolved substances in the opposite one.

Fifth, if there is more than one substance in solution, each will tend to diffuse quite independently of all others. Differences in the concentration of each substance, *considered by itself,* are what determine the rate and direction of diffusion of that substance.

Diffusion and Osmosis in the Plant Cell.—It is upon the principles of diffusion and osmosis that the plant depends, not only for the absorption of water and mineral substances from the soil, but for most of the circulation of materials which goes on within the plant body. The structure of a typical plant cell has already been described, and the osmotic interchanges which go on therein may now be considered.

The cell wall in plants is ordinarily composed of cellulose. Like most organic materials, cellulose has the capacity of absorbing water vigorously by *imbibition* and will therefore swell considerably if placed, when dry, in contact with water. This expansive ability of the cell wall is of some value in certain of the plant's activities, as in the germination of the seed, but the wall of an ordinary living cell is moist and has imbibed water to the limit of its capacity. Water, and most substances in solution, pass through this cellulose wall with readiness, and since it ordinarily offers little resistance to diffusion, its osmotic effect is slight.

As has been noted, in the mature plant cell the cytoplasm is dispersed in a thin layer closely pressed against the inner surface of the cell wall, and completely surrounds a large central vacuole, or sap cavity, filled with water in which various substances, sugars usually prominent among them, are dissolved. On its outer surface next the wall, and on its inner surface next the sap cavity, the cytoplasm is bounded by a delicate membrane, so that here are fulfilled all conditions necessary for osmotic activity —one solution, in the sap cavity, separated by a membrane (or membranes) from another solution, which may be the soil water (in the case of a root hair) or the sap solution of an adjacent cell.

These cytoplasmic membranes offer marked resistance to the diffusion of certain substances, and thus are highly important in cell physiology. They are characteristically semi-permeable, preventing the diffusion of such substances as sugar, which are dissolved in the sap cavity; and the cell, as already noted, is thus able to retain these valuable materials within itself and to use them as a means for bringing in osmotically a continuous supply of water from the soil or from adjacent cells. To the essential mineral salts and to many other dissolved substances, however, these membranes are generally permeable, though in varying degrees, and the cell is therefore readily able to absorb a supply of such substances from any adjacent solution. It has been found by experiment that the degree of permeability of the living cell membranes is not a fixed and constant one but is subject to change from moment to moment in response to changes in the environment or in the protoplasm itself. A cell which at one time admits a given substance very readily may at another allow it to enter but slowly, or may exclude it altogether. Many of the physiological activities of the cell are doubtless regulated by changes in the permeability of its membranes.

The rapidity with which a substance passes through a membrane is due not only to these differences in permeability but to differences in the concentration of the solutions on the two sides of the membrane. Where this difference is great (as noted above) osmotic diffusion will be more rapid than where it is slight. Therefore if the concentration of a dissolved substance within a cell is reduced, either by its diffusion into an adjacent cell or by its conversion into an insoluble form (as must occur when it enters into the construction of a complex organic molecule in the protoplasm), the rate at which a new supply enters the cell from

without is at once correspondingly increased; but the moment its concentration becomes equal within and without the cell, the movement of this particular substance ceases, even though others are passing rapidly through the membranes.

The Absorption of Water and Salts.—This activity of the cell as an osmotic system controls all interchange of material between the cell and its environment. It is of particular importance in the absorption of water and salts from the soil, since the structures by which these functions are performed are typical living cells. Each root hair is a projection from one of the surface cells of the root. The cytoplasm and sap cavity of the basal part of this cell extend into the root hair, so that the latter is thus lined by a thin layer of cytoplasm, with its membranes. The root hair penetrates the soil and comes intimately in contact with the soil particles, to the surface of each of which a thin capillary film of water normally adheres. In this water are dissolved a great variety of substances, notably mineral salts; and each of these will diffuse into the root hair provided that its concentration in the soil solution is greater than its concentration in the sap solution; and provided also that the cytoplasmic membranes will allow it to pass. In this way the plant absorbs from the soil the mineral nutrients which it uses. This entrance of salts, as noted above, takes place *quite independently* of the movement of water. Furthermore, any substance which is in greater concentration in the cell sap than in the soil water, and to which the membranes are permeable, will of course diffuse outward into the soil; but except in the case of carbon dioxide, which is produced in considerable quantities as a result of respiration in the root cells, there is comparatively little loss of material from the plant in this manner.

The total concentration of the soil solution is normally less than the total concentration of the sap solution in the root hair, since in the latter there are ordinarily dissolved considerable amounts of sugar and organic acids. In obedience to the law of diffusion, therefore, water will pass from the soil, where it is relatively more abundant, through the cytoplasmic membranes of the root hair and into the cell sap, where it is relatively less abundant. This flow of water will continue so long as there is a difference in total concentration between soil solution and sap solution. Of course, if the soil becomes dry and the film around each particle grows so thin that the surface attraction of the

particle equals the diffusive force of the water, the flow will cease; and if this condition occurs throughout the whole soil mass, the plant will suffer from drought. If by any chance the soil solution becomes more concentrated than the sap of the root hair, water will necessarily pass out into the soil, and the plant will be injured speedily.

As water is taken into the sap cavity of the root hair, the solution there becomes less concentrated, and the next inner cell is consequently able to withdraw water osmotically from the root-hair cell. The next row of cells may now withdraw water from the first, and this process will continue until the water reaches the fibro-vascular cylinder. The water ducts here, however, are nothing but dead shells, their living cytoplasm having disappeared as soon as the thick cell walls were completed. They are filled with water, and what causes water to move into them from the cells of the cortex rather than in the reverse direction is not well understood. In the innermost layer of cortical cells, a considerable pressure is probably developed by osmosis, and water may simply be squeezed through the cytoplasm and into these ducts. It is known, at any rate, that water is forced up through the ducts under a good deal of pressure, and this *root pressure* may be measured by a gauge attached to an opening in the stem. The causes of the rise of water to great heights in the trunks of trees will be discussed later; but root pressure is apparently only one of the factors there involved.

Other Osmotic Phenomena in the Plant.—Not only the absorption of water from the soil but the whole process of circulation within the plant body, as well, is primarily an osmotic one for the salts taken in by the root hairs, and any dissolved substances in other cells throughout the plant, move from cell to cell by diffusion through the cytoplasmic membranes.

Still another contribution of osmosis to the plant's activities lies in maintaining the turgidity of the tissues. It is evident that if a cell has a strong sap solution and is thus able to absorb water vigorously, it will become plump and fully expanded and will press tightly against its neighbors. If all the cells become turgid in this way the whole plant will tend to be erect and rigid, like an inflated balloon. In the case of parts which do not possess a firm skeleton, such as leaf blades, floral organs, or other comparatively soft structures, this turgidity is necessary to maintain their form, firmness, and proper functioning. Conversely, if a

cell is exposed to a solution of greater concentration than that of its cell sap, water will be withdrawn from it, it will collapse, and its cytoplasm will be pulled away from the walls. Such *plasmolysis*, if extreme or long-continued, will result in the death of the cell; and if extensive, in the death of the plant.

Osmosis also plays an essential part in growth, for at any growing region there is a point where the cells are multiplying in number but are still small, and another point behind this where each expands rapidly to its final size. This expansion, with the consequent stretching of the cell walls and growth of the tissues, is apparently due to the rapid absorption of water by the young and delicate cells, the sap of which is rich in dissolved sugar. The force exerted by any growing region is thus primarily that of osmotic pressure.

Other Functions of the Root.—The root has been discussed briefly as an organ of anchorage and of storage, and in more detail as an organ of absorption. It has, less frequently, certain other functions which should be mentioned. In many climbing plants roots are produced abundantly on the aerial organs and serve to hold the plant firmly to its support. In corn, stout roots arise from the stem at some distance above the ground and pass into the soil, thus acting as props or guy ropes for the tall plant. In epiphytes, the roots are sent out directly into the air and possess a characteristic spongy envelope which absorbs and holds rain water and dew. In parasitic plants the roots are converted into short sucking organs, penetrating the host plant and withdrawing therefrom the food upon which the parasite lives.

QUESTIONS FOR THOUGHT AND DISCUSSION

60. Through what various agencies does bare rock gradually become covered with soil?

61. Is soil always formed from the rock which lies directly under it? What was the origin of the soil in this region?

62. In what various ways is soil becoming impoverished or "used up," and in what various ways is it being replenished?

63. What is the surface of a bit of gravel which is in the form of a solid cube the sides of which are 1 centimeter long? What would be the surface of this bit of gravel if the cube were cut up into smaller cubes with sides 1 millimeter each? What conclusion can you draw from this as to the importance to plants of the size of soil particles?

64. Why do soils in which the particles are small usually produce more vigorous plant growth than do soils in which the particles are larger?

65. What disadvantages are there to plants in soils where the rock particles are very small? What disadvantages where they are large?

66. Why is it harmful to the soil to till (or "work") it immediately after a rain or while the soil is very wet?

67. Which will absorb and hold a larger amount of water: clay or sand? Explain.

68. Will the rise of water by capillarity be higher in sand or in clay? Explain.

69. Which is better for plant growth in a dry season, a clayey soil or a sandy one? Explain.

70. A potted plant dries out the soil in its pot very uniformly, even though its roots fill only a small part of the pot. Explain.

71. Why does the surface of soil which has been perfectly dry during the day often turn moist at night?

72. Why is the soil surface in arid regions often caked with a crust of salts?

73. Which will generally be colder, a soil with fine particles or one with coarse? Explain.

74. Explain exactly why a mulch on the soil surface reduces loss of water from the soil through evaporation.

75. Why is it advisable to scratch over a garden with hoe or rake as soon after a rain as the soil is workable?

76. What advantages are gained by pressing down the soil above seeds after planting them?

77. After sowing seed for certain crops, a farmer often rolls the soil with a heavy roller. What is gained by this practice?

78. Give three reasons for pressing the soil firmly about the roots of a plant after it has been transplanted.

79. The surface of soil after it has been plowed is a few inches higher than it was before plowing. Explain.

80. Why is it necessary to drain wet land before ordinary crops can be grown thereon?

81. In what ways is the air in the soil being constantly changed and renewed?

82. Of what use is air in soil in addition to providing oxygen for plant roots?

83. In what respects is the composition of the air in soil likely to differ from ordinary atmospheric air?

84. State two reasons why the formation of a "crust" on the soil surface is harmful to plants.

85. How is the supply of humus maintained in soils which are not under cultivation?

86. Why is dark-colored soil usually richer than light-colored soil?

87. The continual addition to the soil of no other fertilizers than the ordinary mineral or "commercial" ones is generally found to be harmful. Explain.

88. Why do most commercial fertilizers contain nitrates, phosphoric acid, and potash, but often nothing else in the way of plant nutrients?

89. A good crop of corn, wheat, or potatoes removes about 50 pounds of nitrogen per acre from the soil. Nitrogen composes about four-fifths of the weight of the atmosphere. At this rate of removal by crops, how many years would the nitrogen in the air over an acre last, provided that it could be made available to the plants growing there?

90. Why are wood ashes so valuable as fertilizer?

91. What two important contributions to human welfare are made by the bacteria of decay?

92. Plants native to the woods will often fail to thrive when transplanted to a garden, even though the soil there is rich and the conditions of shade and temperature are much like those in the forest. What reason can you suggest for this difficulty?

93. Vegetable growers often sterilize by steam, formalin, or other means the soil in the greenhouse beds where they are to grow their young plants for later transplanting outside. What advantages has this process? What disadvantages would it have if applied in the field?

94. Farmers sometimes build a bonfire over the spot where they are going to start their young plants of cabbage, tomato, and similar crops. What two advantages are gained by this?

95. State at least three advantages which are gained by plowing the soil.

96. Plants which have very deep roots (such as certain weeds and cover-crop plants) are sometimes of advantage to crops which are subsequently grown on the same soil. Explain.

97. Land which is left uncropped or "fallow" for a few years is found to be more productive when cultivated again. Explain.

98. A "cover crop" is one which is planted in late summer or early fall and grows up enough to cover the ground before winter. It is often plowed under the next spring. What are the advantages of planting such a crop?

99. Why is extensive removal of forests often followed by floods?

100. Why is flood-plain or river-bottom soil usually very productive?

101. Which is ordinarily more symmetrical in shape, the root system of a plant or its stem system? Explain.

102. Tap roots are usually tapering in shape, being broadest next the surface of the ground and gradually narrowing below. Explain.

103. In a young plant growing from seed the root is larger and better developed at first than the stem or leaves. Explain.

104. The fibro-vascular system of the root is usually in the form of a solid rod, and that of the stem in the form of a hollow tube. Of what advantage to the plant are these arrangements of the tissues?

105. Why does a covering of grass turf or other close plant growth prevent the erosion of soil on steep banks and other exposed situations?

106. If a tree trunk is partially buried (through raising the level of the soil about it by grading, for instance) why is the tree likely to die?

107. Desert plants tend to have very deep root systems and bog plants very shallow ones. Explain these facts.

108. Roots will usually grow toward a supply of nutrient material in the soil. What causes them to do this?

109. Of what advantage are root hairs to the plant aside from their function in the absorption of water and mineral nutrients?

110. Why are root hairs entirely absent on the older portions of the root?

111. Why are root hairs absent from the growing region near the tip of the root?

112. Why are root hairs commonly absent in water plants?

113. If a sac made of bladder or a similar osmotic membrane is filled with molasses, tied up, and placed in a vessel of water, what will happen?

114. If this same sac is filled with water, tied up, and placed in a vessel of molasses, what will happen?

115. If two solutions are separated by a membrane, under what conditions will water pass through the membrane without any movement of dissolved substances taking place? When would this be likely to happen in the root hairs of plants? Explain.

116. Under what conditions will a given dissolved substance pass through a membrane without any movement of water taking place? When would this be likely to happen in the root hairs of plants? Explain.

117. Under what conditions will water pass through a membrane in one direction and a given dissolved substance in the other? When would this be likely to happen in the root hairs of plants? Explain.

NOTE.—In the five following questions, assume that the sac is made of an elastic membrane which is semi-permeable in that it allows the free diffusion of water but entirely prevents the diffusion of sugar. Assume further that the membrane is readily permeable to dissolved salt. State clearly what will happen under the conditions set forth in each question, carrying the process through to its conclusion and noting the differences, if any, between early and later stages.

118. What will happen if the sac is filled with a solution of sugar and placed in a vessel of pure water?

119. What will happen if the sac is filled with a solution of sugar and the liquid in the vessel is a solution of salt which is of lesser concentration than the sugar solution in the sac?

120. What will happen if the sac is filled with a solution of sugar and the liquid in the vessel is a solution of salt which is equal in concentration to the sugar solution in the sac?

121. What will happen if the sac is filled with a solution of sugar and the liquid in the vessel is a solution of salt which is greater in concentration than the sugar solution in the sac?

122. What will happen if the sac is filled with a mixture of sugar and salt solutions of equal concentration and the liquid in the vessel is pure water?

123. Do you think that a plant can take out all the water from the soil around its roots? Give reasons for your answer.

124. Why will the stems of many woody plants "bleed" if cut in the early spring but will not do so if cut in the summer?

125. Water is sometimes forced from the leaves of a plant in the form of droplets. Why is this, and under what conditions would you expect it to take place?

126. Why do tomatoes and other soft and fleshy fruits tend to split open in a wet season?

127. How do submersed water plants get their salts?

128. Why is it that a plant can take up such large amounts of salts when these salts occur in such very weak concentrations in the soil?

129. Many plants thrive for long periods without extending their root systems into regions of fresh soil. How are they able to obtain an unfailing supply of nutrient salts under these conditions?

130. A plant grown in "water culture" (in a jar of water containing the necessary mineral salts in solution) will remove the salts from the jar almost completely, even though its roots fill only a small portion of the jar. Explain.

131. Iodine is much more abundant in the tissues of certain sea-weeds than it is in the sea water. Explain how this can be.

132. How is it possible for a group of cells in the middle of a tissue, surrounded by other cells, to contain large amounts of a given substance which is rare or absent in the adjacent cells?

133. The text states that the cytoplasmic membranes of a root hair are impermeable to sugar, and that sugar therefore cannot get out of the root hair into the soil. If this is true, how do you explain the fact that sugar was able to get into the root hair in the first place?

134. The salts taken from the soil by one plant are often very different in kind and amount from those taken in by another plant. To what factors may such differences be due?

135. Why does one crop often require different fertilizer treatment from another?

136. Why will some fertilizers, if applied very abundantly, often kill plants?

137. Why is a strongly concentrated spray solution likely to kill the plants to which it is applied?

138. It sometimes happens that a spray solution which will kill one plant does not kill another. Explain.

139. Why will strong spray often kill the young and growing parts of a plant when it does not kill the older portions?

140. If a very strong spray (such as lime-sulphur, used against certain bark insects of fruit trees) is to be applied to a tree, why must this be done only when the tree is leafless?

141. In such places as gravel walks and tennis courts it is often customary to kill weeds by sprinkling salt upon them. Why is this practice effective? Why is it not widely used in killing farm weeds?

142. How is it possible for some plants to live in salt marshes and on sea beaches, while most plants cannot?

143. How is it possible for a plant to suffer from drought in a soil abundantly supplied with water?

144. Desert plants and salt-marsh or sea-beach plants frequently show similar modifications in structure. Explain.

145. Why is a person thirsty after eating much salt or sugar?

146. The sap concentration in the cells of parasitic plants has been found to be higher than in the cells of the plants upon which they are parasitic. Explain.

147. Celery, sliced cucumbers, and similar vegetables are often placed in water for a while before being served. What effect does this produce, and why?

NOTE.—In the four following questions, remember that decay is due to the activity of bacteria, which are small plant cells.

148. Why is salt such a good preservative of vegetables, meat, fish, and other foods?

149. Old-fashioned preserving of fruit was done by the "pound-for-pound" method, a pound of sugar being used for every pound of fruit. Why was this method successful even in the absence of boiling or any other means of sterilization?

150. Which will "keep" better if freely exposed to the air, grape juice or grape jelly? Explain.

151. What is the fundamental difference between preserving food by salt and preserving it by benzoate of soda or a similar "preservative" substance?

152. What causes root hairs to force themselves in among the soil particles?

153. Growing roots and stems often exert tremendous pressures, sometimes sufficient to split and lift heavy rocks. What causes this expansive power?

154. Rocks are sometimes split apart, in quarrying, by the insertion of dry wooden wedges into cracks or drills. These wedges are then wetted and their swelling exerts a powerful pressure. How different in its origin is this pressure from that exerted by a tree root in splitting open a rock?

REFERENCE PROBLEMS

31. What is *irrigation?* How and under what conditions is it practiced?

32. Describe the agricultural practice known as the "rotation of crops." What is its value?

33. Describe the principles and practice of "dry farming."

34. Soils which are poorly aerated are likely to be "sour." Why is this true? What measures may be taken to correct it?

35. Distinguish between animal manures, green manures, and commercial fertilizers, and state the advantages and disadvantages in the use of each.

36. What benefit to plants may fertilizers confer aside from providing a supply of mineral nutrients?

37. Why is the problem of providing a sufficient supply of nitrate salts for agricultural fertilizers not as serious as it was a few years ago?

38. Rice is exceptional among cultivated plants in using nitrogen chiefly in the form of ammonia compounds rather than nitrates. Why should this be so?

39. What is the chemical formula of atmospheric nitrogen? of ammonia? of potassium nitrate? of some organic nitrogenous compound?

40. To what extent may *organic* substances (complex materials derived ultimately from living organisms) enter directly into ordinary green plants and be used by them as food?

41. Give an example of a crop plant which thrives best on alkaline soil; one that thrives best on acid soil. Which of these two soil types do most crop plants favor? What reason is there for this fact?

42. About how many bacteria are normally present in one cubic centimeter of rich soil?

43. What various types of root-tubercle bacteria are there? Will all of them infect all species of leguminous plants?

44. Give the author and title of three important books on the soil, and outline briefly the content of each.

45. State the chemical composition of the ash of three important crop plants, taking your figures from any reliable determinations. How does it happen that the substances and their proportions are different in the different plants?

46. What is the difference between a *nutrient* and a *balanced* solution for plant growth?

47. What scientists were chiefly responsible for our present understanding of osmotic phenomena and their application in plant physiology?

48. Give the author and title of three important books dealing with plant roots, or with the mineral nutrition of plants, and outline briefly the content of each.

49. Name several botanical investigators who have done important work on the structure of roots or on the absorption of water and mineral nutrients by roots; and state the notable contributions made by each.

50. Give the derivation of the following terms and explain in what way each is appropriate:

Capillarity	Mycorhiza	Imbibition
Humus	Diffusion	Plasmolysis
	Osmosis	

CHAPTER V

THE LEAF AND ITS FUNCTIONS

The vegetative organs of the plant naturally fall into two groups: the root system, situated in the soil and concerned primarily with the absorption therefrom of water and certain nutrient materials; and the stem and leaves (together called the *shoot*), which unfold in the air and are concerned primarily with the manufacture of food, the raw materials for which they derive both from the air and from the soil. Of the two members of the shoot system the leaf is the primary and more important one, the stem serving chiefly to expose the leaves to light and air and to provide a means of communication between them and the root. It is logical, therefore, to follow the study of the root with that of the leaf.

Before the functions of the leaf can be understood, it is necessary to have clearly in mind the important facts with regard to its structure.

External Structure (Figs. 36 and 37.)—The largest and most conspicuous portion of a typical leaf is the *blade*, a broad, flat, and thin sheet of green tissue, in which its most important activities are carried on. This is provided with a system of ribs or *veins*, which are stouter than the rest of the blade and serve to support the softer tissues between them. They are also connected directly with the fibro-vascular system of the stem and root, and thus bring up to all parts of the leaf the water and salts used there and carry back to the rest of the plant the products of photosynthesis. The blade may sometimes be attached directly to the stem (in which case the leaf is said to be *sessile*), but more frequently it is supported by a leaf stalk or *petiole*, which holds it out in a position favorable for food manufacture and serves as a highway for transportation between blade and stem. At the base of the petiole, on either side of the point where it is attached to the stem, there sometimes occur two small appendages, the *stipules*. These may protect the young blade in the bud, serve as subsidiary food-manufacturing structures, or become transformed into spines or glands. Their function is

often obscure, and in many families of plants stipules are absent entirely.

Leaves vary widely in size, shape, texture, margin, venation, and other characters. In size they range from small scales, as in the arbor vitae, to the immense leaves of some tropical plants, the blades of which may be several meters long. All gradations in shape are found, from leaves which are *linear* (long and narrow), as in the grasses, to those which are almost circular in outline, as in the nasturtium. Between these two general types many

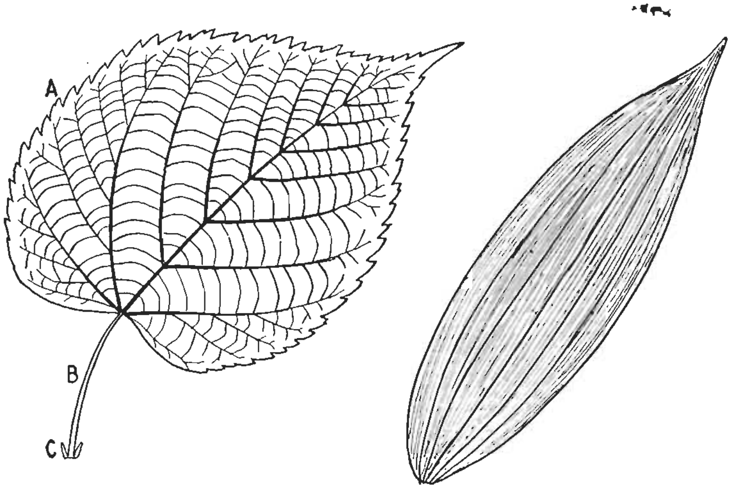


FIG. 36.—Two types of leaf venation. At left, netted-veined leaf of linden: *A*, blade; *B*, petiole; *C*, stipules. At right, parallel-veined leaf of Solomon's seal.

shapes, both of the blade as a whole and of the outline of its tip and its base, are recognized and named. The edge or margin of the leaf may also vary greatly. In some, as in rhododendron or corn, this is quite smooth or *entire*, and in others it is provided with *teeth* of various sizes and shapes. In certain leaves, such as most maples and oaks, the indentations are still deeper, and produce a leaf which is *lobed*. In the most extreme cases, the blade may be so deeply lobed that it is divided into separate parts, in which case the leaf as a whole is said to be *compound*, and its parts are called *leaflets*. If the leaflets all are attached at a common point, as in clover, the leaf is *palmately* compound; if they arise in pairs along the continuation of he petiole (called the *rachis*), as in mountain ash, it is *pinnately* compound (Fig. 37*A*). The arrangement of the veins is also variable. There are two

main types (Fig. 36): *parallel* venation, where the veins run side by side with no conspicuous branches; and *netted* venation, where they divide repeatedly and form a complicated and interconnected network throughout the blade.

The leaf surface is sometimes smooth and shining, but in many plants it is covered, to a greater or less degree, with a coating of hairs of various sorts. When these occur rather thickly, they are

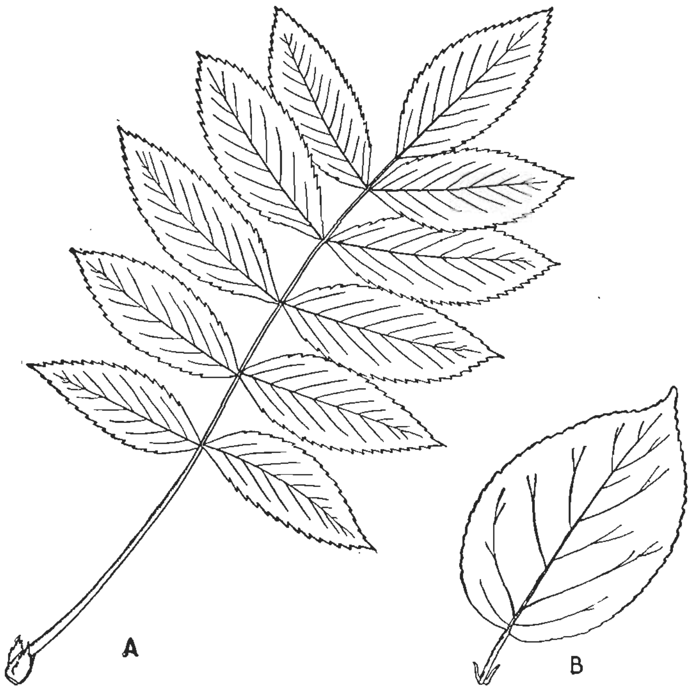


FIG. 37.—Simple and compound leaves. *A*, compound leaf of mountain ash, with eleven leaflets. *B*, simple leaf of apple.

believed to reduce evaporation from the leaf surface; in other cases they produce glandular secretions; and less frequently they may function as stinging organs, as in the nettle.

The typical foliage leaf has often been modified, during the course of evolution, to perform functions quite different from the primary one of photosynthesis. Some leaves have been reduced to bud scales, which protect the young growing points, as in most woody twigs; others are modified into spurs, as in the barberry; others are reduced to thick, food-storing structures, as in the scale leaves of the onion bulb; others store water, as in the stonecrops;

and still others serve to capture insects, as in the sundew, pitcher-plant, and bladderwort. In certain underground stems, as the tubers of the potato, the leaves are reduced to tiny vestiges; and in parasitic plants like the dodder, they also are minute and seem quite functionless.

Leaves arise as lateral outgrowths of the stem, and are developed at the terminal growing point. In many cases they are fully formed while very small, as is the case in most winter buds. Unlike stems, typical leaves have no organized growing points, and after they have reached mature size they neither grow further nor produce new structures from their tissues. In perennial plants they ultimately die and drop off.

Internal Structure.—Internally the structure of the leaf is marked by a high degree of differentiation. A transverse sec-

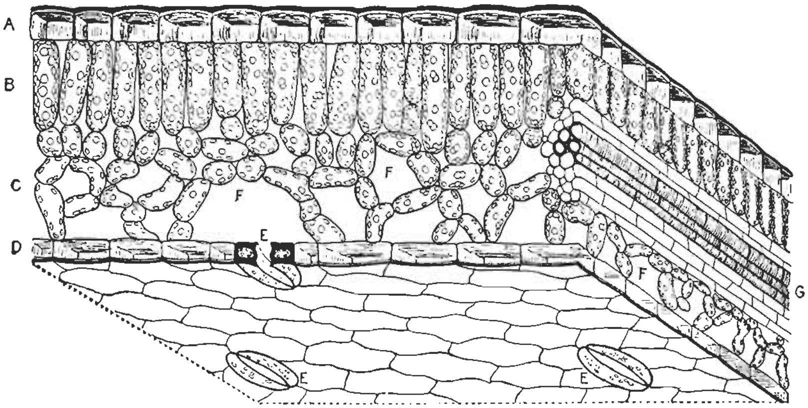


FIG. 38.—A small piece of a typical leaf blade, seen in three planes and highly magnified. *A*, upper epidermis, covered by the cuticle (in black); *B*, palisade layer; *C*, spongy layer; *D*, lower epidermis, covered by cuticle; *E*, stomata, the one in the lower epidermis shown in section; *F*, intercellular air space; *G*, vein, cut lengthwise.

tion cut at right angles to the surface of the blade (Figs. 38 and 39) displays three types of tissue. These are the *epidermis* or protective covering; the *mesophyll*, constituting the major portion of the leaf substance; and the *veins*, each of which is a fibrovascular bundle and a branch of the vascular system which runs through root and stem.

The epidermis, which is usually but a single cell-layer in thickness, protects the delicate mesophyll tissues against mechanical injury, loss of water, infection, and other harmful environmental

influences. Its cells are filled with a transparent cell sap, and their outer walls are often markedly thickened and somewhat convex. Spread over their surfaces is a thin, waxy, water-proofing layer, the *cuticle*, extending from cell to cell, and ordinarily much thicker on the upper than on the lower surface of the leaf.

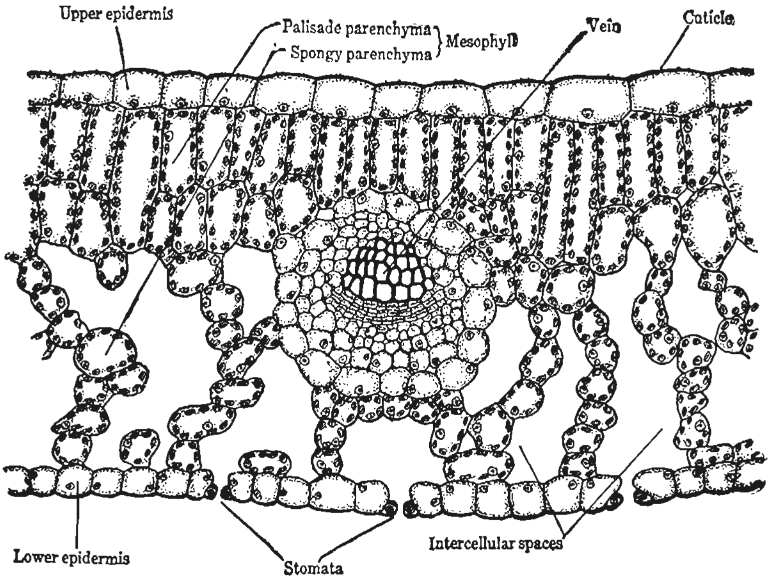


FIG. 39.—Cross section through the blade of a privet leaf. (*From Haupt.*)

The epidermis is not an unbroken layer, but is provided with minute openings, the *stomata* (singular, *stoma*), through which an exchange of gases between the tissues of the leaf and the air outside may take place (Fig. 40). These are generally much more numerous in the lower epidermis than in the upper, and may often be quite absent from the latter. Each stoma is a slit-like pore caused by the separation, along part of their surface of contact, of two specialized epidermal cells, the *guard cells*. These are so constructed that when plump and turgid with water they tend to pull apart (although still in contact at their ends) and thus produce an opening between the cells. On becoming limp and partially collapsed, however, they spring together again and close this opening. The degree of stomatal opening is thus continually fluctuating as the water content of the guard cells rises and falls in response to changing internal or external conditions.

The guard cells are unlike other cells of the epidermis in that they contain chloroplasts.

On the epidermis of the leaf (and often of the stem, as well) there are frequently developed unicellular or multicellular outgrowths, the *hairs* or *trichomes* (Fig. 41). These are of several sorts and may perform a variety of functions.

The mesophyll consists of tissue which is characteristically thin walled, soft, and green. The cytoplasm within its cells contains great numbers of very small, roundish bodies, the *chloroplasts,* which are denser than the rest of the living substance and

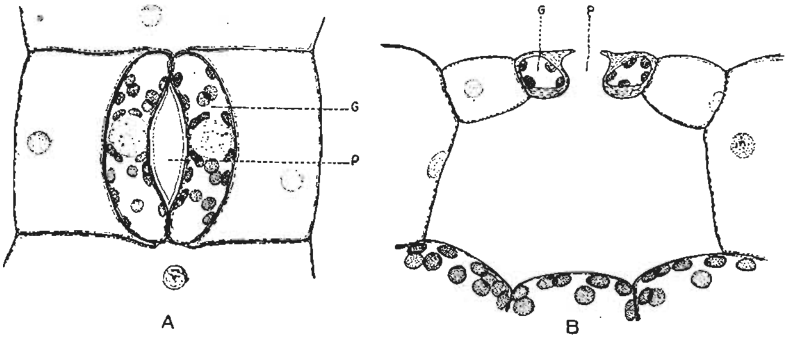


FIG. 40.—A stoma. *A*, face view, showing the guard cells (G) containing chloroplasts; the pore (P) or opening between the guard cells; and the adjacent cells of the epidermis to which the guard cells are attached. *B*, transverse section, cut at right angles to the longer dimension of the stoma, showing the large air space into which the pore leads.

contain within them the green pigment *chlorophyll,* to which the characteristic color of foliage is due, and which is so essential in the process of photosynthesis.

The mesophyll is not a homogeneous tissue, but in most leaves is divided into two main regions. The portion lying next to the upper side of the leaf is composed of cells elongated at right angles to the leaf surface and packed rather closely together (Fig. 42). They are provided with a great abundance of chloroplasts, estimated at over 400,000 per square millimeter of leaf surface in some cases. This region is known as the *palisade* layer, and here is carried on most actively the process of photosynthesis. The lower region of the mesophyll, on the other hand, consists of cells which are but loosely in contact, with the result that large air spaces occur between them, and a very loose, sponge-like tissue, the *spongy layer*, is produced. These air spaces com-

municate directly with the outside air through the stomata. Chloroplasts are present in the spongy layer, but much less frequently. Through the exposure to the air of a large area of cell

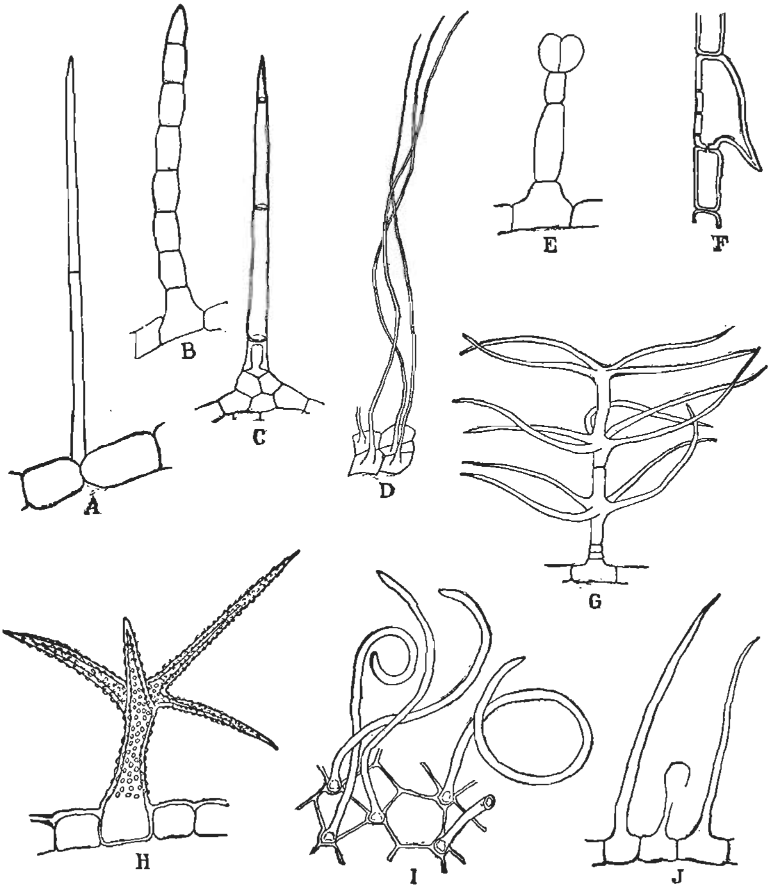


FIG. 41.—Various types of plant hairs. *A*, from corolla of *Epigaea; B*, from leaf of *Coreopsis; C*, from leaf of *Cucumis; D*, from stem of *Onopordum; E*, from corolla of *Phryma; F*, from leaf of *Avena; G*; from young leaf of *Platanus; H*, from stem of *Aubrietia; I*, from fruit of *Rubus; J*, from calyx of *Heliotropium*. (*From Eames and MacDaniels.*)

surface, opportunity is provided in this tissue of the mesophyll for those gas exchanges which are continually taking place between the leaf and the atmosphere, such as the absorption and release of both carbon dioxide and oxygen in the processes of photosynthesis and respiration, and the evaporation of water in

transpiration. The arrangement of mesophyll tissues here described is characteristic of leaf blades which are horizontal or approximately so, but in vertical leaves, such as those of many grasses, it is much modified, and there is a palisade layer on both leaf surfaces (Fig. 43).

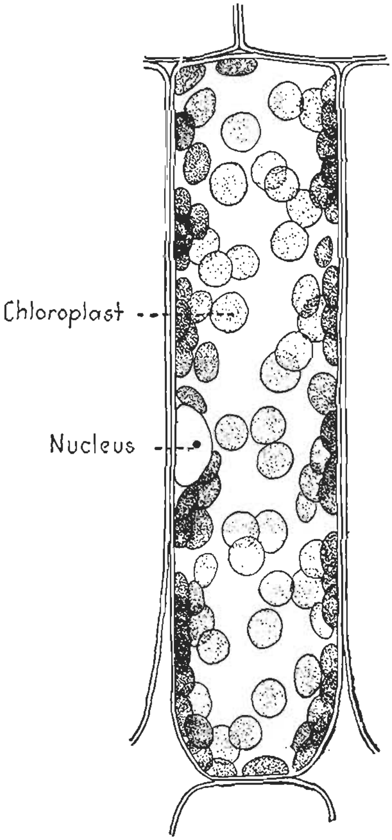


FIG. 42.—A cell from the palisade layer of the leaf. The chloroplasts are somewhat biscuit-shaped bodies, roughly circular in face view and elliptical when seen from the side. They are imbedded in the thin and transparent layer of cytoplasm, their broad faces parallel to the cell wall.

Running through the blade are the veins or fibro-vascular bundles, channels by which the leaf tissues communicate with the rest of the plant. The main veins are stout, often projecting somewhat below the lower surface of the blade. These break up into smaller and smaller bundles, and finally into minute veinlets consisting of only a few cells, in intimate contact with the cells

of the mesophyll. Each vein is surrounded by a bundle sheath, which in the larger veins may include some thick-walled cells to which much of the rigidity of the vein is due, but which in the smaller veins consists of simple, thin-walled elements acting as intermediaries between the conducting tissue and the mesophyll cells. The bundle itself is made up of two tissues. These are the wood (xylem) consisting largely (as elsewhere in the plant body) of elongated, water-conducting cells, the *ducts* and *tracheids*, which distribute the water and dissolved substances brought up through the stem from the root; and the phloem (bast) consisting of specially modified cells, the *sieve tubes*, which collect from the mesophyll the foods manufactured there and convey

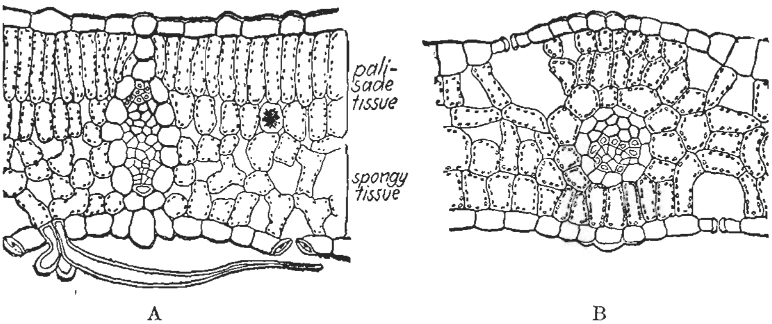


FIG. 43.—Relation of orientation of leaf to its structure. *A*, cross section of a leaf which is typically horizontal (oak); *B*, cross section of a leaf which is typically vertical (oat). Leaves of the latter type tend to have a palisade layer on both surfaces. (*From Eames and MacDaniels.*)

them to the phloem of the stem and thus to other parts of the plant. In a horizontal leaf, the wood of the vein is toward the upper surface and the phloem toward the lower surface of the blade.

The petiole, usually circular or essentially so in cross section, has within it an arc of fibro-vascular bundles which are continuous with the main veins of the blade above and which enter directly into the vascular cylinder of the stem below.

Photosynthesis.—The primary activity of green leaves is the *manufacture of food* from certain simple inorganic materials—carbon dioxide and water—by energy derived from light. This process of *photosynthesis* is fundamental in organic nature, for it is not only an essential function of green plants themselves but is of the utmost significance to animals and man, since it constitutes the sole ultimate source of food in the world. Food

is primarily a storehouse of *energy* and of *body-building materials* for living things. In the green parts of plants active or *kinetic* energy—in this case the energy of light—is converted into a latent or *potential* form, readily available to living organisms for use in maintaining their vital activities; and, moreover, in green plants alone are produced those fundamental organic materials out of which plant and animal bodies are constructed. The complex metabolic changes which later take place in the organic world are simply elaborations or amplifications of the primary products of photosynthesis. A more detailed account of the various types of foods, of their uses, and of the energy relations of the plant, will be presented in the chapter on Metabolism.

Materials.—The materials combined by the plant in this process are but two—water and carbon dioxide. Water is absorbed from the soil by the roots, passes upward through the stem, the petiole, and the veins of the leaf, and thence enters the mesophyll cells. None is obtained by the leaf directly from the atmosphere. It should be remembered that only a relatively small portion of the water taken in by the plant is used in food manufacture, for much the larger part soon leaves the plant again, passing out of the leaf into the air by transpiration. The carbon dioxide used in photosynthesis is derived entirely from the air. Here it is always present, but in such small quantities that it constitutes only about three parts in ten thousand by volume of the atmosphere, or three hundredths of one per cent. Experiments have shown that a higher concentration is advantageous to plant growth, since up to a certain point the rate of photosynthesis rises if the proportion of carbon dioxide in the air is artificially increased. It is through this comparatively rare gas alone that the plant derives its supply of carbon, that element so vitally necessary to all living organisms. No other carbon compounds, not even the abundant supplies present in the complex organic materials of humus, can apparently be drawn upon by most green plants. Carbon, oxygen, and hydrogen, together with the essential elements derived from the soil, constitute the necessary chemical basis for plant life.

Mechanism.—The mechanism or apparatus by which water and carbon dioxide are combined is the remarkable green pigment *chlorophyll.* This is present in the *chloroplasts,* specialized portions of the cytoplasm slightly denser than the rest. Chloro-

plasts may be relatively large in some of the lower plants, but in the higher forms they are very small and numerous, and are usually somewhat spherical in shape. They are most abundant in the cells of the palisade layer of the leaf, but occur in all green portions of the plant body.

As to chlorophyll itself and exactly how it works, comparatively little is known. Chlorophyll is a complex protein, thus being composed of carbon, hydrogen, oxygen, and nitrogen; and in addition it contains magnesium. Iron is essential for its production, but does not enter into its composition. Light also is usually necessary for the development of chlorophyll, as is shown by the pale color of leaves which have grown in darkness. Furthermore, chlorophyll is not a homogeneous substance, but has been found to consist of two very similar but distinct pigments known as *chlorophyll a* and *chlorophyll b*. The former is blue-green in color and more abundant than the latter, which is yellow-green. The following approximate chemical formulae have been determined for these two substances, and give an idea of their constitution and of the differences between them:

Chlorophyll *a*, $C_{55}H_{72}O_5N_4Mg$
Chlorophyll *b*, $C_{55}H_{70}O_6N_4Mg$

It is noteworthy that these pigments are very similar chemically to the haemoglobin of blood, iron in the latter taking the place occupied by magnesium in the former.

Chlorophyll of both types has the remarkable physical property of *fluorescence*, whereby its color as seen by reflected and by transmitted light is quite different. When a solution of chlorophyll, freshly extracted from a leaf, is held up to the light it appears to be green. When placed against a dark background, so that light is reflected from it, it is a deep red. This property is shared by only a few other pigments.

Almost invariably associated with chlorophyll in the higher plants are two other pigments, yellow in color, and very much alike. These are *carotin*, containing carbon and hydrogen; and *xanthophyll*, probably derived from it and containing, in addition, a little oxygen. The function of these pigments is not well understood. If they are concerned at all with photosynthesis they apparently play a much less important part than does chlorophyll. They are responsible for most of the yellow colors which occur in plants. Unlike chlorophyll, which is a

very unstable compound and tends to break down quickly when extracted from the leaf or when the cells containing it lose their vitality, these yellow pigments are very resistant and often survive long after chlorophyll has disappeared.

How chlorophyll operates in bringing about the union of carbon dioxide and water is unknown, but since it does not contribute to the product formed and is not itself used up in the process, one may infer that it acts as a catalyzer. Recent successful experiments in effecting the union of carbon dioxide and water outside the plant and in the absence of chlorophyll indicate that photosynthesis may be carried on by other agents, and may in time perhaps be accomplished artificially on a large scale.

Energy.—Energy is necessarily expended in the process of breaking up the molecules of water and carbon dioxide and recombining their atoms into a new compound. Since experiment readily proves that photosynthesis will never take place in darkness, regardless of what the other environmental conditions may be, it is clear that the form of energy employed is always *light,* a fact which explains the very important part which light plays in the physiology of plants.

According to the most widely accepted theory, light is due to minute and enormously rapid vibrations, the length of the vibration—its *wave length*—determining the color of the light produced. Sunlight, or any white light, is composed of vibrations of a great variety of different wave lengths, but when such light is passed through a prism these become sorted out into a many-colored *spectrum.* The visible spectrum runs from the red rays, the wave length of which is approximately 750 millionths of a millimeter, to the violet ones, where it is approximately 400. These visible radiations are by no means the only ones which occur, however. Rays of longer wave length than red—the infra-red rays—pass gradually into heat waves, and those shorter than violet—the ultra-violet rays—are active chemically. When falling upon different objects, light behaves differently. All of it may be absorbed by the object and converted into heat or some other form of energy, the object then appearing black; or all may be reflected, the object then appearing white; or certain wave lengths may be absorbed and certain others reflected, the object in such a case displaying to our eyes the color of the light which it reflects. A green substance like

chlorophyll, for example, absorbs in general those wave lengths which are not green and reflects those which are green or greenish-yellow. One can determine more accurately, however, the kind of light which is absorbed by a substance if he breaks up into a spectrum the light which has passed through that substance. Such a spectrum displays perfectly dark regions, or *absorption bands,* in those portions which correspond to the particular kinds or wave lengths of light which the substance has absorbed. The

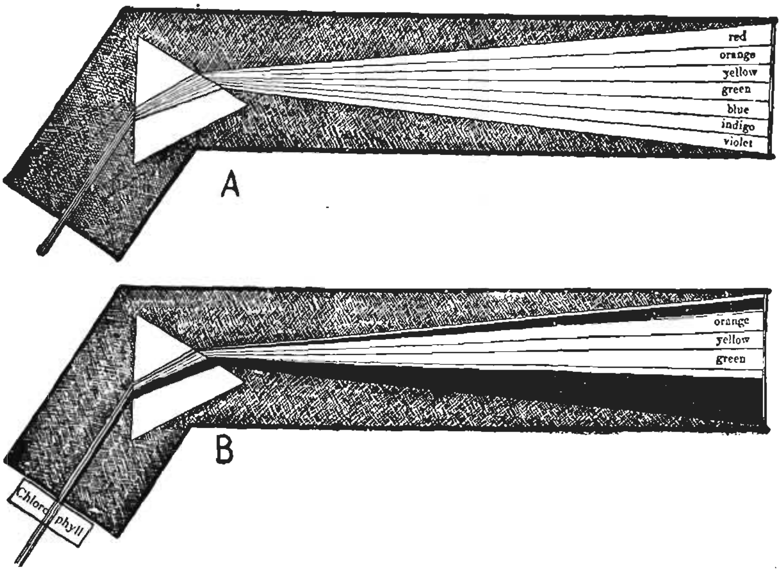


Fig. 44.—Diagrams showing light broken up by the prism of a spectroscope into its constituent portions, which form a spectrum. *A*, spectrum of white light; *B*, spectrum of light which has passed through a chlorophyll solution, showing the dark "absorption bands" in the red and the blue. (*From Ganong, "The Living Plant," Henry Holt and Co.*)

absorption spectrum of chlorophyll (Fig. 44) shows a narrow, sharp, black band in the orange red and a wider, less definite one in the blue, thus indicating that it is chiefly these two kinds of light which chlorophyll absorbs, and suggesting that the red and blue rays in sunlight, and no others, furnish the energy used in the process of photosynthesis. That this is the case is readily proved by projecting a spectrum upon the surface of a leaf which has been kept for a time in the dark, and which receives no other illumination; and by testing this leaf, after a time, for starch. Under these conditions starch is found only in those areas of

the leaf which were illuminated by the red and the blue portion of the spectrum. Most experimental evidence seems to indicate that photosynthesis ordinarily takes place more actively in the red light than in blue, probably because of the greater energy-supplying power of all rays at this end of the spectrum. Portions of the spectrum which are not visible to our eyes (infra-red and ultra-violet), however important they may be in other physiological processes, apparently take little or no part in photosynthesis.

The intensity as well as the character of the light affects the rate at which photosynthesis proceeds. It begins at illuminations of very low intensity, reaches its maximum with most plants at about that of bright diffuse daylight, and decreases again in light which is so strong as to be injurious. Plants differ considerably in the intensity of light necessary for photosynthesis, some being able to thrive and grow at illuminations far too weak to suffice for others. Photosynthesis may readily be carried on in artificial light of the proper character and intensity.

Only a very small part, estimated at from .5 to 3.0 per cent of the total amount of sunlight falling upon the leaf, is actually utilized in food manufacture and locked up in potential form, so that photosynthesis is a relatively inefficient process. The total area of all leaf surface exposed to the light is so great, however, and the source of light so powerful, that the actual amount of energy absorbed and used by chlorophyll in the aggregate is enormous. It not only constitutes the sole source of energy for the vital processes of plants and animals, but the most important source for industry, as well.

Products.—The details of the process whereby carbon dioxide unites with water are not yet known, but the formation of formaldehyde (CH_2O) is perhaps one of the preliminary steps. The first product which can be recognized, however, is usually *glucose* or *grape sugar*, $C_6H_{12}O_6$, formed according to the following equation:

$$\underset{\text{Carbon dioxide}}{6CO_2} + \underset{\text{Water}}{6H_2O} = \underset{\text{Glucose}}{C_6H_{12}O_6} + \underset{\text{Oxygen}}{6O_2}$$

Glucose is present in the sap of practically all plant cells. It is the fundamental carbohydrate and the basis for all other foods; and from it are ultimately derived, through the action of

enzymes and by various additions and chemical modifications, all the organic compounds of plants and animals.

The presence of a large amount of sugar in a chlorophyll-bearing cell results in a stoppage of its manufacture there, and is disadvantageous for other reasons. It is found, accordingly, that before photosynthesis has long continued, the resulting sugar becomes converted into another type of carbohydrate, *starch* $(C_6H_{10}O_5)_n$.* Starch is complex and insoluble, occurring in minute but definite bodies or *grains*, the size, shape, and markings of which are characteristic and constant in any plant species. The starch molecule is very large—just how large is not known—and is derived through the combination of many glucose molecules, with the liberation of a molecule of water from each, thus:

$$\underset{\text{Glucose}}{n(C_6H_{12}O_6)} - \underset{\text{Water}}{n(H_2O)} = \underset{\text{Starch}}{(C_6H_{10}O_5)_n}.$$

Neither sugar nor starch are accumulated in very great quantities in the leaf blade, for most of the products of photosynthesis are removed shortly after their production to those regions of the plants where they are to be used or stored.

The rate at which photosynthesis takes place and at which these products are formed depends on many factors, among the more important of which are the amount of chlorophyll exposed to light; the size, number, and degree of opening of the stomata; the quality and the intensity of the light; the amount of carbon dioxide available; the temperature; and the rate at which the product is carried away from the leaf. It has been found that the amount of new material (chiefly sugar and starch) produced by a square meter of leaf surface of a healthy plant varies, roughly, from half a gram to two grams per hour.

By-product.—In the recombination of the atoms of carbon dioxide and water out of which glucose is produced there must evidently be a surplus of oxygen. This is given off as a by-product of photosynthesis, passing forth continuously from green plants during their exposure to light. This fact is of little significance to the plant itself, but often is important to other organisms.

Significance of Photosynthesis.—Photosynthesis is, therefore, a constructive process by which the food of the plant is manu-

* *n* stands for the unknown number of smaller molecules which are united into one of the large and complex ones of such a substance as starch.

factured from very simple inorganic materials, through the agency of the characteristic substance chlorophyll, and by energy derived from light. Its significance lies in the fact that it is the only process among living things whereby organic compounds are built up from simple inorganic substances, with the resultant storage of energy. All other chemical changes in plants and animals are concerned either with the transformation of one type of organic material into another or with the breaking down of complex organic compounds into simpler ones. Photosynthesis alone is fundamentally constructive, and the activity of green plants thus underlies that of all other organisms.

It was not until relatively recent times that this process was well understood. Priestley in 1772 discovered that if plants were grown for a time in air which was incapable of supporting combustion or respiration, the air became "purified" once more. Ingenhousz proved that this effect was produced only by the green parts of plants and in the light. Senebier established the fact that carbon dioxide is absorbed, and the modern conception of photosynthesis was established finally by de Saussure early in the nineteenth century.

The fact that green plants in the light seem to be taking in carbon dioxide and giving off oxygen, and that these same plants in darkness clearly are taking in oxygen and giving off carbon dioxide, renders this aspect of plant physiology somewhat confusing. It should be remembered that the latter process (which is known as *respiration*) is being carried on by every living cell at all times and under all conditions; but that the former process (photosynthesis) although intermittent, ordinarily is so much more active during the period in which it is carried on that at such times respiration is completely masked and seems not to be taking place at all.

Transpiration.—The lower portion of the mesophyll, or the spongy layer, is not concerned primarily with photosynthesis but with the interchange of gases between plant and atmosphere. Notable among these interchanges is the evaporation of water from the tissues and its passage into the air, a process known as *transpiration.*

The Importance of Water.—The water relations of a plant are of the utmost importance to it and profoundly influence its structure and activities. Water constitutes the major portion (75 to 90 per cent) of plant tissues in general, and a much larger

share of protoplasm itself. An abundance of water keeps the cells plump, and by maintaining the turgidity of the tissues, enables the soft parts of the plant to preserve their firmness and to function successfully. Water is one of the raw materials entering into the process of photosynthesis. It is the solvent of the mineral nutrients, which can enter the plant and move about within it only when in solution; and in watery solutions all the important physiological processes of the plant take place. The maintenance of an abundant supply of water in its tissues is therefore essential for the life and growth of the plant.

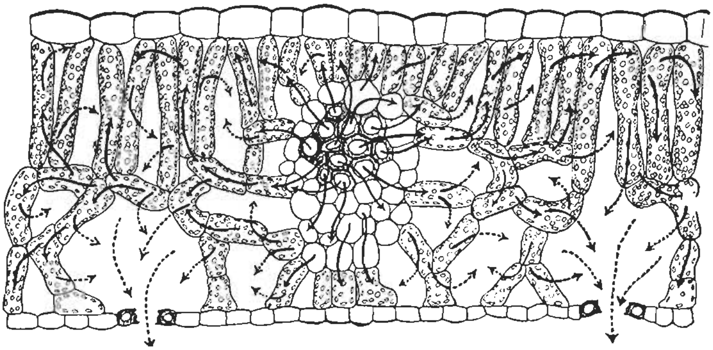


FIG. 45.—Transpiration from the leaf blade. Cross section through a blade including a vein. Arrows indicate passage of water from the vein through the mesophyll cells into the air spaces and out through the stomata. Solid arrows indicate liquid water; dotted arrows, water vapor.

To this end the primary requisites are evidently the presence of a sufficient amount of available water in the soil and its abundant absorption therefrom by the roots. Of no less significance in the water relations of the plant is the process by which this water evaporates from the plant tissues and passes into the air. Absorption must equal or exceed transpiration if the plant is to thrive, for should there be a deficiency in income or an excess of outgo, a shortage of water will result in the tissues and the plant will suffer accordingly.

Only a very small fraction of the water which enters the root hairs and passes upward to the leaves takes part in the manufacture of sugar. The remainder becomes distributed through the cells of the spongy layer and evaporates from their moistened walls, departing through the stomata as water vapor (Fig. 45). A smaller amount may be evaporated directly from the surface of the epidermal cells. During the growing season a

constant stream of water is thus passing through the plant body, entering at the root hairs and departing through the stomata. The total quantity of this water usually amounts to several hundred times as much as the final dry weight of the plant itself (Fig. 46).

FIG. 46.—Rate of transpiration. The amount of water transpired from this corn plant, during its growth and development, would under normal conditions fill the barrel.

The Rate of Transpiration.—The rate of water loss varies greatly according to the kind of plant, the soil conditions, the season of the year, the time of day, and various environmental factors. As a general rule, the rate tends to increase under conditions which favor increased evaporation, such as high

temperature, bright light, rapid air movement, and low humidity; and to decrease under environments of the opposite character.

Transpiration is by no means controlled entirely by factors which influence evaporation alone. The rate of water loss from a given leaf surface and from an equal area of free water do not rise and fall exactly together, the transpiration from the living leaf sometimes being relatively higher and sometimes relatively lower. There must, therefore, be factors within the leaf itself (as opposed to those in the external environment) which tend to accelerate or retard transpiration. The most important of these is doubtless the opening and closing of the stomata, which has already been discussed. Changes in the concentration of the sap in the mesophyll cells also probably determine to some extent the rate at which water evaporates from their surfaces.

The actual amount of water transpired during the growing season may be large or small, depending on the size of the plant, its leaf area, its transpiration rate, and the moisture and fertility of the soil. Of most significance to the plant, however, is not the actual bulk of transpiration but the efficiency of the plant in its water relations. This is determined by comparing the weight of the total water transpired with the weight of the dry plant material produced, the quotient obtained through dividing the former quantity by the latter being termed the *water requirement* of the plant. Thus when it is said that the water requirement of corn under certain environmental conditions is 400, it is meant that for every gram of dry weight of corn plant produced at maturity, there have been transpired through its leaves 400 grams of water. Species vary markedly in their water requirements, and so do plants of the same species when grown under different environments.

The Significance of Transpiration.—Excessive water loss is an ever-present danger to land plants, and many structural modifications have been developed by various species, or may appear in particular individuals growing under dry conditions, which tend to reduce this loss. The question therefore arises as to whether transpiration is an unmixed evil, made necessary by the fact that the stomata must be open to allow the exchange of gases which takes place in photosynthesis; or whether it is really a function of the leaf and performs a useful part in the plant's economy. It was long thought that water must be taken in through the roots in large quantities to insure an abundant absorption of

nutrient materials from the soil, but a fuller understanding of the phenomena of osmosis and root absorption shows the fallacy of this conclusion. It has also been contended that transpiration is useful in concentrating the very dilute solutions of nutrient salts taken from the soil—"boiling them down," so to speak. It has been shown, however, that the factors which determine the entrance of nutrient materials into the plant preclude such an explanation; and, indeed, experiment proves that the amount of salts absorbed is practically independent of the amount of water transpired. Transpiration from the leaves, however, is evidently what causes the *transpiration stream* or continuous movement of water from root to leaf through the lifeless ducts in the wood of the stem. This movement will be more fully considered when the functions of the stem are discussed, but it is well to note here that in this stream the dissolved substances are transported bodily from the central cylinder of the root upward through the plant as far as the ramifications of the wood extend. This movement is probably far more rapid than would result through diffusion from cell to cell; and in tall plants, particularly, the transpiration stream may perform a distinct service in distributing rapidly throughout the plant the supply of mineral nutrients absorbed from the soil.

Transpiration seems also to be of some use in regulating the temperature of the leaf. The blade absorbs much more energy than it uses in photosynthesis, particularly in bright light; and the excess, as heat, would at times probably raise the temperature of the tissues dangerously were it not absorbed in evaporating water from the mesophyll cells.

Transpiration is carried on primarily in the leaves but may occur in any other organs which are exposed to the air. Excessive loss of water is often prevented in such regions by the development of cell layers with corky walls.

QUESTIONS FOR THOUGHT AND DISCUSSION

155. Why are leaves generally more variable in area than in thickness?

156. What general difference in shape is there between netted-veined and parallel-veined leaves?

157. Leaves on the same plant often differ markedly in the length of their petioles. Explain.

158. In leaves where the veins are much stouter than the thickness of the blade, they usually stand out on the *under* side of the leaf and thus leave the upper surface smooth. What are the advantages to the plant of this arrangement?

159. For plants of temperate climates, of what advantage and of what disadvantage is it to shed their leaves in the winter?

160. The leaves of evergreen trees do not remain permanently on the tree, but each year's crop lives only a few seasons and then drops off. Why should these leaves not continue to live and function indefinitely?

161. Why are the upper epidermis and its cuticle almost always thicker than the lower?

162. The cells of the leaf epidermis usually have transparent walls and a colorless cell sap. Of what advantage is this to the plant?

163. In the vein of the leaf, why is the woody portion toward the upper surface and the phloem toward the lower? (For a suggestion, see Fig. 52.)

164. How do you explain the fact that the palisade layer is next the upper surface of the leaf and the spongy layer next the lower?

165. Of what advantage is it for the cells of the palisade layer to be elongated at right angles to the leaf surface?

166. Do you think that photosynthesis is carried on in the spongy layer at all? Give evidence for your belief.

167. Name at least two advantages which the plant derives from having its stomata more abundant on the lower surface of the leaf than on the upper.

168. Why are stomata usually absent on the leaves of submersed water plants?

169. Why does washing the leaves of house plants often improve the health of the plants?

170. In cities where soft coal is burned and there is thus much coal dust in the air, all trees suffer and evergreen trees, in particular, find it very difficult to live. Explain these facts.

171. In what ways is the supply of carbon dioxide in the atmosphere being replenished?

172. Do you think that the continual removal of carbon dioxide from the atmosphere by green plants through photosynthesis will reduce the amount of that gas which is present there? Explain.

173. The great deposits of coal formed in the coal period, millions of years ago, have sometimes been cited as evidence that carbon dioxide was much more abundant in the atmosphere then than now. What basis is there for such a conclusion?

174. As the carbon dioxide in a leaf is removed by photosynthesis, what causes a fresh supply to enter through the stomata from the outside air?

175. In some greenhouses the plants are "fertilized" by pouring carbon dioxide from a chimney into the air around the plants. Why does this increase plant growth and why is it usually impracticable out-of-doors?

176. The fact that carbon dioxide is more soluble in cold water than it is in warm has been cited as one of the reasons why seals, walruses, polar bears, and even Eskimos are able to thrive so far north. Explain.

177. Which is ordinarily darker green in color, the upper or the lower surface of the leaf? Explain.

178. Why does the intensity of green color in its foliage provide good evidence as to the health of a plant?

179. In variegated leaves, the areas free from chlorophyll are not as well developed as the green areas. Explain.

180. The stems and leaves of parasitic plants, such as mistletoe and dodder, are either very pale green or some other color than green. Explain.

181. Why do autumn leaves and dying leaves often turn yellow?

182. When cows are turned into fresh pasture in the spring, their butter turns a deeper yellow. Explain.

183. In order to "bleach" celery plants, gardeners cover them with earth or wrap them in paper. Why is this practice effective in securing the desired result?

184. What is the orientation (vertical, horizontal, oblique, or other) of an ordinary leaf blade? Explain.

185. In many herbaceous plants the lower leaves have long petioles, but higher up on the stem the petioles gradually decrease in length and often are quite absent from the uppermost leaves. Explain.

186. Of what advantage and of what disadvantage is it for a plant to have its leaves deeply cut or lobed?

187. Are opposite leaves usually broader or narrower than spirally arranged ones? Explain.

188. Why is it easier to maintain a lawn under elms or apple trees than under maples?

189. In just what part of the crown of a tree are most of its leaves borne? Explain.

190. Why do the lower limbs of a tree growing in the forest usually die?

191. Many plants are able to thrive in relatively deep shade on the floor of the forest, where the lower limbs of the forest trees have long since died. How can this be?

192. Seedlings of most forest trees will grow on the forest floor in rather deep shade, but the lower limbs of mature trees of the same species, if subjected to similar light conditions, will soon die. Of what advantage to the plant is this difference between young and old individuals?

193. What factor, in addition to weak light, may be concerned in the scarcity of small plants (herbs and low shrubs) in a forest?

194. Most of our woodland wild-flowers (herbaceous plants which grow on the forest floor) thrive and blossom in early spring, and often die away during the summer. Explain.

195. Why are south windows best for plants which are growing indoors?

196. Leaves exposed to bright sunlight are usually thicker than those growing in the shade, even on the same plant. Explain.

197. Plants in greenhouses in the winter rarely grow as rapidly as they do out-of-doors in the summer, even if the temperature is the same. Explain.

198. Why do most plants grow faster in June than later in the summer, even if there is no difference in temperature or rainfall between the two seasons?

199. Crops are necessarily planted much later near the northern limit of their range than farther south, but in many cases their growth rate is so much more rapid that they reach maturity almost as soon. Explain.

200. In the North Sea fisheries, it has been found that the size of the season's catch of fish tends to be greater in seasons when there has been much sunshine than in seasons which have been relatively cloudy. Explain.

201. Will a plant thrive better in red light or in green light? Explain.

202. Other things being equal, is it better to plant the rows of a garden east and west, or north and south? Explain.

203. Some plants (such as the fungi) are able to thrive in the absence of light. What other important physiological differences must there be between these and ordinary green plants?

204. Of what advantage is it to the plant to have the sugar which is produced by photosynthesis converted rapidly into starch?

205. It is sometimes said that forests tend to "purify the air." What basis in fact (if any) is there for this statement?

206. Why do animals in an aquarium thrive better if green water-plants are growing in the aquarium?

207. If a spectrum of white light is thrown on a filament of green alga which is otherwise in the dark, and if bacteria are present in the water around the alga, it has been observed that these bacteria will tend to gather more abundantly around those parts of the algal filament which are illuminated by the red light and the blue light than they do elsewhere. Explain.

208. Which do you think will be worse for a tree, the loss of half of its branches by an ice storm or all of its leaves through an insect attack? Explain.

Note.—By the term *dry weight* is meant the weight of all the material in a given body except its water. It is usually determined in the laboratory by drying the material in an oven at about 100° C.

209. Will the dry weight of a leaf ordinarily be greater in the morning or in the late afternoon? Explain.

210. Would you expect seedlings grown in the dark to increase in actual weight? in dry weight? Explain your answer.

211. Why are the leaves of parasitic plants usually very small?

212. How are submersed water plants able to carry on photosynthesis?

213. Give at least three reasons why trees often fail to thrive in a city.

214. Some crops produce a much larger amount of dry weight per acre than others. Explain how this can be.

215. The potato beetle does not attack the potato tuber but eats only the foliage of the potato plant. Why does it harm the crop?

216. Why does repeatedly cutting off their tops finally kill persistent perennial weeds?

217. If one wishes to clean out "suckers" and low shrubs from pasture land, should he mow them down in summer or in winter? Explain.

218. What basis in fact is there (if any) for the belief held by some farmers that there is a particular day in summer when suckers and brush should be cut down if one wishes to kill them out?

219. Why should a new field of asparagus not be harvested until two or three years after the young plants have been set out?

220. Which should be kept mown more closely, a newly-seeded lawn or an old one? Explain.

221. Should lawn grass, when cut, be raked off the lawn or not? Explain.

222. State two reasons why a garden planted near a shade tree is likely to be unsatisfactory.

223. Do you think that transpiration is essential for the life of a plant? Explain.

224. What process in animals may be said to correspond roughly to the transpiration of plants? In what respects are the two processes similar?

225. From your knowledge of osmosis, explain why it is that "the amount of salts absorbed is practically independent of the amount of water transpired by the plant."

226. Just where in the leaf does evaporation take place during the process of transpiration?

227. What makes water leave the cytoplasm of the spongy-layer cells (or any others) and wet the cell walls?

228. Why is it that the air in the air spaces of the spongy layer of the leaf does not become so saturated with moisture that evaporation, and consequently transpiration, will no longer take place?

229. In general, the faster a plant loses water through transpiration, the faster it will absorb it from the soil. Explain.

230. Will transpiration be more rapid or less rapid if the sap of the mesophyll cells increases in concentration? Explain.

231. Why does transpiration take place faster in wind than in still air?

232. Why do florists usually water the walls and walks of a greenhouse as well as the plants themselves?

233. Why does a plant wilt if its water supply fails?

234. Some plants wilt much more readily than others. What factors may be responsible for this difference?

235. Why is a wilted plant unable to carry on its functions as well as one that is in a normal, turgid condition?

236. Why does a plant sometimes wilt in a hot day even though the soil in which it is growing is abundantly supplied with water?

237. Why does a plant which has wilted in the daytime usually revive at night, even though no rain falls?

238. If a tree is subjected to a severe drought its leaves wilt but its twigs remain rigid. Explain.

239. In using cut foliage for decorations, would you choose young leaves or mature ones? Explain.

240. The stomata often tend to close in the middle of a hot day. Why is this, and how is it of advantage to the plant?

241. Do stomata tend to open or close if the leaf is exposed to light? Explain.

242. How will stomata tend to act during the course of a normal period of twenty-four hours during the summer?

243. What is the best time of day to pick flowers, if it is desired to keep them fresh for a long time out of water? Explain.

244. Why will cut flowers remain fresh longer if they have been placed in water for a few hours directly after being picked?

245. Do you think that the water requirement of a plant will be higher if it is grown on rich soil or if it is grown on poor soil? Explain.

246. Assuming that the water requirement of corn under a given set of conditions is 400, and that a bucket holds 10 liters, how many buckets of water have passed by transpiration through a corn plant the dry weight of which is 200 grams?

247. Given the same conditions as in the previous question, assume further that three such corn plants are planted in each hill and that the hills are one meter apart each way. If all the water which passes through these plants by transpiration during the season could be collected, how deep a layer would it make over the surface of the field?

248. Why does a shortage of water stunt a plant?

249. Is transpiration likely to be high or low when growth is most rapid? Explain.

250. Why do plants generally grow faster in wet weather than in dry?

251. Why do plants generally grow faster at night than in the daytime?

252. How do you reconcile the fact that plants grow faster at night than in the daytime with the fact that light is necessary for the manufacture of food?

253. The planting of rank-growing species like the sunflower has sometimes been thought to reduce the amount of malaria in malarial districts. What basis in fact is there for this belief?

254. It has been observed that springs in a forest sometimes begin to flow more abundantly after the leaves fall from the trees in autumn and continue to do so until the next season's crop of leaves has come out, when they dry up again. Explain these facts.

255. Why is the effect of a killing frost usually not evident on the following morning until the sun has been up for some time?

256. The leaves of corn and other grasses often roll or curl when it is very hot or dry. Why is this, and of what advantage is it to the plant?

257. The leaves of desert plants are usually leathery, fleshy, or very small. Explain.

258. The leaves of *Eucalyptus*, a tree which flourishes in warm, dry regions, hang vertically on the branches. How is this of advantage to the plant?

259. The leaves of "compass plants" are erect and vertical, with their edges pointing approximately north and south. How may these characters be of advantage to the plant?

260. Plants with downy or wooly leaves are abundant on mountain sides and exposed alpine situations. How are they particularly suited to such conditions?

261. Why do epiphytes (page 202) usually have leathery leaves?

262. Why are the leaves of evergreens in temperate regions usually firm and leathery?

263. Evergreen trees often suffer from "wind burn" in early spring, a part or all of their branches dying and turning brown. They rarely suffer from this cause earlier or later in the season. Explain.

264. Give two reasons for the fact that plants grown in the shade are usually more tender than plants grown in bright sunlight.

265. Tobacco growers sometimes cover their plants with cheese-cloth tents. What effect do you think this has on the structure and activity of the tobacco leaves?

266. Why is early spring better than summer as a time to transplant trees?

267. Why is it better to transplant on a cloudy or rainy day than on a bright one?

268. Why is it advantageous to cut off the outer leaves of young plants before transplanting them?

269. If it is necessary to transplant trees during the summer, why should they first be vigorously pruned?

270. Why will potatoes in storage lose weight much faster after sprouts have grown out on them?

REFERENCE PROBLEMS

51. What various functions may stipules perform? Give an example of each.

52. What various functions may plant hairs perform?

53. Give the number of stomata per square centimeter of leaf surface on three species of plants.

54. What is the chemical composition of ordinary air? How many cubic centimeters of air are needed to provide enough carbon dioxide for the manufacture of one gram of starch by photosynthesis?

55. How does the efficiency of the leaf in utilizing the energy of sunlight compare with that of a steam engine in utilizing the energy from burning coal?

56. In the case of some one common crop plant, give the percentage of water, of dry matter, and of ash which typically compose it. From what source has each been derived?

57. What chemical relationship is there between chlorophyll and haemoglobin? What suggestion can you make as to the reason for this relationship?

58. Describe experiments which have been successful in effecting the photosynthetic union of carbon dioxide and water outside the plant body.

59. What is the average annual rainfall in this region? In a field on which a vigorous crop of plants is growing, about how much of this rainfall is returned to the air by transpiration?

60. Give the water requirement of three common crop plants when grown under ordinary conditions.

61. What are the "rain trees" found in some parts of the tropics and what is the physiological explanation of their behavior?

62. What is an atmometer and how is it used in investigations on plant transpiration?

63. Give the author and title of three important books dealing with leaves or their functions, and outline briefly the content of each.

64. Name several botanical investigators who have done important work in the fields of photosynthesis or of transpiration, and state the notable contributions made by each.

65. Give the derivation of the following terms and explain in what way each is appropriate:

Petiole	Epidermis	Chlorophyll
Stipule	Stoma	Xanthophyll
Mesophyll	Photosynthesis	Transpiration

CHAPTER VI

THE STEM AND ITS FUNCTIONS

The root, which absorbs water and mineral nutrients from the soil, and the leaf, which carries on the manufacture of food, are the primary vegetative organs of the plant. A third member, the *stem*, connects these two. It forms a conspicuous feature of most plants and in woody species constitutes the largest portion of their bodies. Its functions, though in a sense secondary to the major activities mentioned above, are nevertheless essential ones. It supports the leaves, disposing them in situations favorable for the carrying on of photosynthesis; and it serves as a highway for the transportation upward of water and mineral nutrients from the root system to the aerial portion of the plant, and *for the transportation of manufactured food from the leaves* downward to regions where it is to be consumed or stored. The stem also holds up the flowers and fruit in favorable positions and conducts to them the materials necessary for their growth. In addition, it frequently serves as a place of food storage, and it may become variously modified for food manufacture, water storage, dispersal, reproduction, and other functions. The stem system and leaf system together constitute the *shoot*.

The External Structure of the Stem.—The stem displays a wide range of variation in size and in external structure according to the habit or growth form which the plant assumes. In *herbs* (Fig. 47), where the whole shoot dies back to the ground during seasons unfavorable to growth or at the completion of a life cycle, the stem is comparatively slender and soft in texture, with little corky bark and a fibro-vascular system not strongly developed. In plants with perennial above-ground structures, however, it grows thicker from year to year and develops into the stout and woody axis characteristic of shrubs and trees. In a *shrub* (Fig. 48) the stem is comparatively short and slender, and tends to branch freely, even close to the ground. In a *tree* (Fig. 49) it grows taller and is developed for some distance into a main stem or *trunk*, which may become very thick. Herbs under favorable

conditions may grow into plants with perennial woody stems, and in some species the difference between a shrub habit and a tree habit may also be dependent upon the environment. Thus the castor bean plant, which is an annual herb in temperate regions,

FIG. 47.—An herb. The lark-spur (*Delphinium*).

develops into a stout woody plant in the tropics; and species which are trees in the lowlands may become dwarf shrubs on a mountain side.

Leaves.—Leaves are borne throughout the length of the stem in herbaceous plants, but only on its younger portions in woody forms (Fig. 50). That point on a stem at which a leaf is attached

is known as a *node*, and the region between two nodes as an *internode* (Fig. 51).

The arrangement of leaves on the stem, or its *phyllotaxy*, may display several different types. If but one leaf is borne at a node, the next above it arises from the other side of the stem, and the arrangement is thus an *alternate* one (Fig. 50). These two leaves may be exactly half way around the stem from each

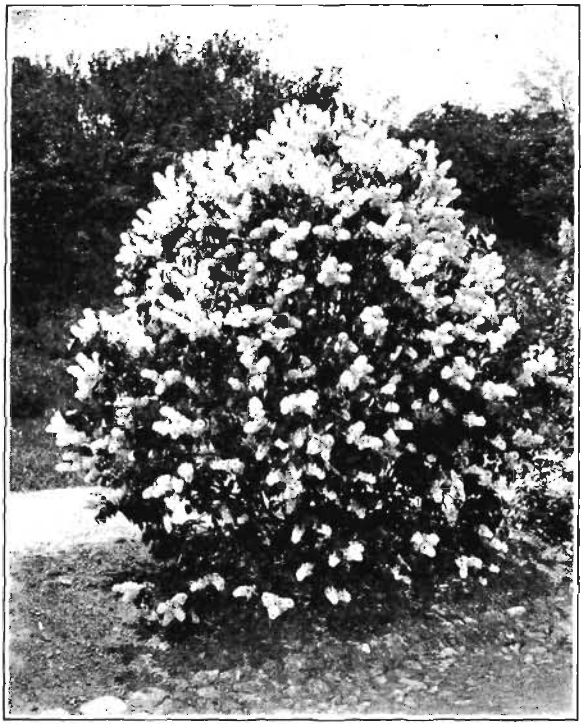


FIG. 48.—A shrub. The lilac (*Syringa vulgaris*).

other, but it is much more common for their angle of divergence to be less than 180° and for the points of attachment of a series of successive leaves thus to form a loose spiral around the stem. The closeness of this spiral and the position of the leaves along it show considerable diversity, but for any particular species are generally constant. If two leaves arise from the same node, they always are directly across the stem from each other, and are said to be *opposite* in arrangement (Fig. 51). When there are

more than two leaves at a node, they are distributed about the stem in a circle or *whorl.*

The advantage of these various types of arrangement is that the leaves are disposed in such a manner that they do not cut off the sunlight from each other and thus interfere with photosynthesis. Furthermore, in whatever position the stem may be placed with reference to the light which falls upon the plant, the

Fig. 49.—A tree. The shagbark hickory (*Carya ovata*). (*Courtesy United States Forest Service.*)

leaves, either by the elongation or the twisting of their petioles, will tend to assume a position where the blade faces the light and occupies a space not shaded by another leaf. Through this "leaf mosaic," obviously, the maximum photosynthetic area is exposed to illumination.

In woody twigs as the time approaches when a leaf is to be shed, a layer of corky cells, the *absciss layer,* is developed across the base of the petiole, just at the point where it is attached to

the stem. The growth of this layer finally causes the fall of the leaf, and at the same time seals over the wound thus produced. The position of these *leaf scars* on a twig thus indicates the former distribution of leaves upon it (Fig. 51).

Surface.—Most young stems are green in color and carry on a certain amount of photosynthetic activity. For a time they are protected by a typical epidermis, but in woody plants this soon

A *B*

FIG. 50.—A woody twig of cherry in summer condition (*A*) and winter condition (*B*). The buds arise in the angle between leaf and stem.

is replaced by a characteristic layer of corky cells, the *bark.* The necessary exchange of gases between the air and the living tissues of the stem takes place through the *lenticels,* small spots or strips where the bark tissue is softer and looser than elsewhere.

Buds.—The growth of the stem in length and the development from it of lateral stems or *branches* takes place only at certain definite points where the cells remain thin walled and capable of active division. These specialized growing points are known as

buds (Fig. 51). In most herbaceous stems, and in woody ones which grow continuously, these buds are not protected; but in

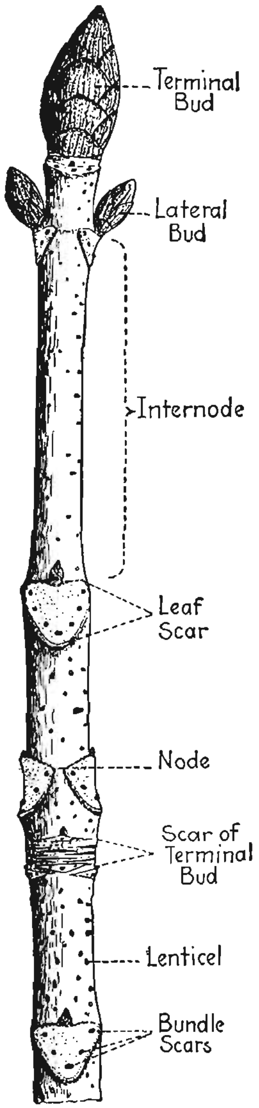


FIG. 51.—A woody twig in winter condition (*Horsechestnut*).

perennial woody plants of temperate climates or other regions where there is a period of inactivity in growth, the buds are

dormant for a time, and are covered by stout and impervious *bud scales*, which are much reduced and modified leaves. These scales drop off when the bud develops, and the scars left by them may often be used to determine the number of growth periods through which the stem has passed, and thus to compute its age.

Buds may be *terminal*, developing at the tip of the stem and governing its elongation; or *lateral*, arising from the sides and determining the position of the branches. A lateral bud ordinarily occurs at each node, arising from the upper angle between leaf and stem, a point known as the *axil* of the leaf. Such buds are often called *axillary* buds. Under certain conditions, usually following the injury or removal of the ordinary terminal and lateral buds, *adventitious* buds may develop from almost any point on the stem, and may even sometimes make their appearance on roots or leaves. In most plants only a few of the buds ordinarily grow, the rest dying or remaining in a dormant state. There are often many dormant buds under the bark which are but slightly developed and never grow unless stimulated by unusual conditions.

Buds may differ in the structures which compose them. In an ordinary *branch bud* (sometimes rather inaccurately called a "leaf bud") there is to be found a much shortened stem with its tiny leaves attached, an entire young branch preformed and ready to grow. *Flower buds* develop into one or more flowers. *Mixed buds* contain both leaves and flowers.

Most stems continue to elongate indefinitely, but in certain herbaceous plants the terminal growing point ultimately produces a flower or flower cluster, and the growth of the stem in length usually ceases at this point. In stems which branch, as in most herbs and all shrubs and trees, the shape of the whole shoot system is determined primarily by the number and arrangement of these branches and by their rate of growth relative to each other and to the main stem.

The Internal Structure of the Stem.—The internal structure of the stem is usually more complex than that of the other plant organs, for its tissues perform the diverse functions of mechanical support, conduction of water, and conduction and storage of manufactured food, and also provide for the continuous growth of the stem in thickness. These functions are centered chiefly in the highly specialized fibro-vascular system, which may be disposed in separate strands or *bundles* (variously distributed),

or may consist of a hollow cylinder. This is directly continuous with the fibro-vascular system of the root, below, (which ordinarily is in the form of a solid cylinder), and with the veins of the petiole and leaf blade above. It consists of two major tissues, the *wood*, or *xylem*, concerned chiefly with mechanical support and the conduction of water; and the *phloem*, (or "*bast*") concerned chiefly with the conduction of manufactured food. The fibro-vascular structures are imbedded in the fundamental ground tissue of the stem, which ordinarily shows but little differentiation and functions chiefly as a seat of food storage. Outside the whole is the *epidermis*, replaced at an early stage by a zone of *corky bark*. These various tissues are represented in the other organs of the plant, but they reach their greatest differentiation and complexity in the stem, and therefore can be more profitably studied in detail in connection with this organ.

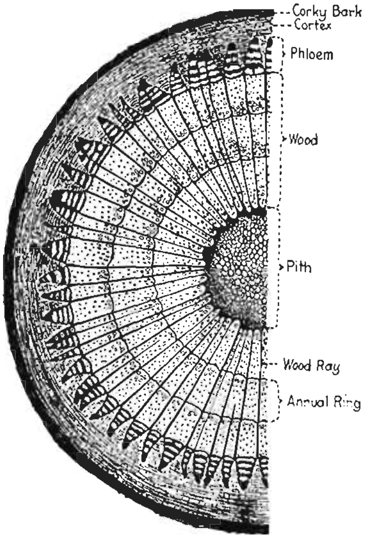


FIG. 52.—Transverse section of a three-year-old twig of the tulip-tree (*Liriodendron*). This is a typical woody stem. The fibro-vascular cylinder consists of a solid ring of wood within and phloem without, surrounding a central pith.

The stem type characteristic of gymnospermous seed plants and of that portion of the angiospermous ones known as the dicotyledons (plants with two cotyledons in the seed, and netted-veined leaves) is probably the primitive form for the seed plants, and differs so markedly from that of the monocotyledons (plants with a single cotyledon and parallel-veined leaves) that the two types will be described separately.

The Stem of Gymnosperms and Dicotyledons.—The arrangement of tissues in the young stem of a woody dicotyledonous plant is shown here in cross section (Fig. 52). On the outside is the *corky bark*, beneath which lies the *cortex*, varying in thickness but rarely occupying as prominent a place in the stem as it does in the root. Beneath this, in turn, is the tubular *fibro-vascular cylinder*, consisting of wood within and

phloem without, and showing (in this twig) three well-marked annual rings. The core of the cylinder is occupied by the *pith* which much resembles the cortex, and, like it, is a part of the ground tissue of the stem.

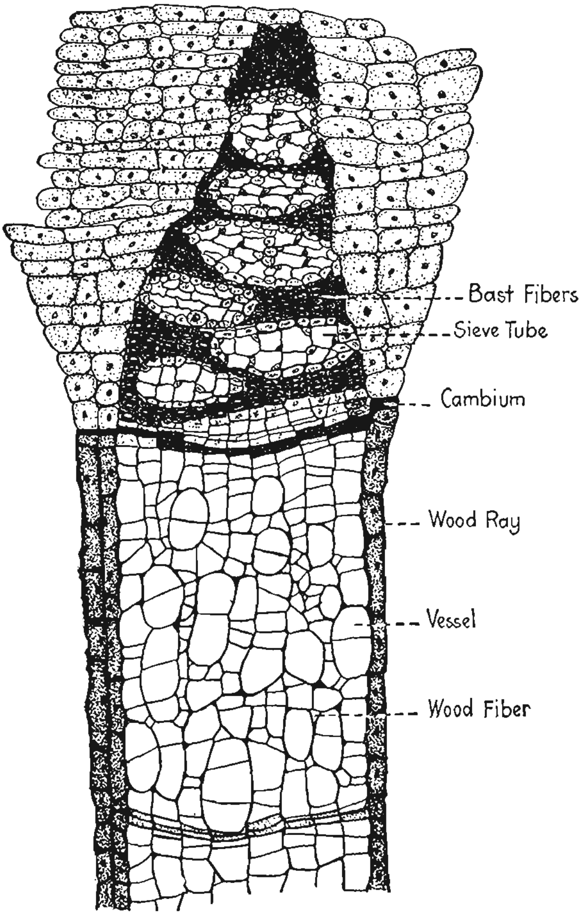


FIG. 53.—A portion of Fig. 52 more highly magnified, including part of one of the segments between two wood rays. The last annual ring of wood, together with one of the groups of phloem cells, is included.

The more detailed structure of these tissues is shown in Fig. 53, which is a portion of the fibro-vascular cylinder in Fig. 52, much enlarged; and in Fig. 54, which is this same region as it appears if cut longitudinally along a radius of the stem.

Protective Layers.—The epidermal cells resemble those of the leaf epidermis and require no special comment. In stems which are growing in thickness, however, the epidermis is soon sloughed off and its protective function is assumed by a layer of corky cells formed directly under it and constantly renewed by the activity

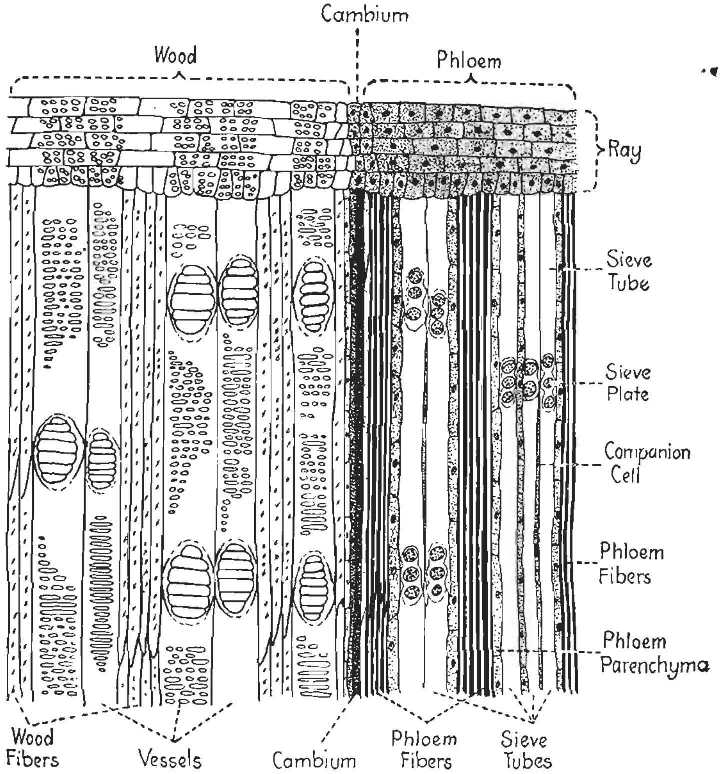


Fig. 54.—Radial longitudinal section of wood and phloem of the tulip-tree, cut through the region shown in Fig. 53. At the left is the wood and at the right the phloem, with the cambium between. The ladder-like markings in the vessels are the end walls of the vessel cells, and the small elliptical markings are pits in their side walls. The ends of the sieve tubes are occupied by sieve plates.

of a *cork cambium* or *phellogen.* In these bark cells the protoplasm soon disappears and the normal cellulose wall becomes corky or *suberized* and is thus rendered almost impermeable to air or water. The *lenticels* (Fig. 55) are small areas in this corky layer where the cells are somewhat loose and spongy and thus allow a small amount of gaseous interchange. The term *bark* is often loosely used to designate all the tissues lying outside the wood.

Cortex and Pith.—The cortex and the pith are very similar in constitution. Their cells are roughly spherical in shape, retain their cellulose walls, and function chiefly in the storage of food. To such undifferentiated tissues the term *parenchyma* is often applied. In older woody stems the pith often dries up and collapses; and the cortex, crushed by the expansion of the wood underneath it, is finally sloughed off.

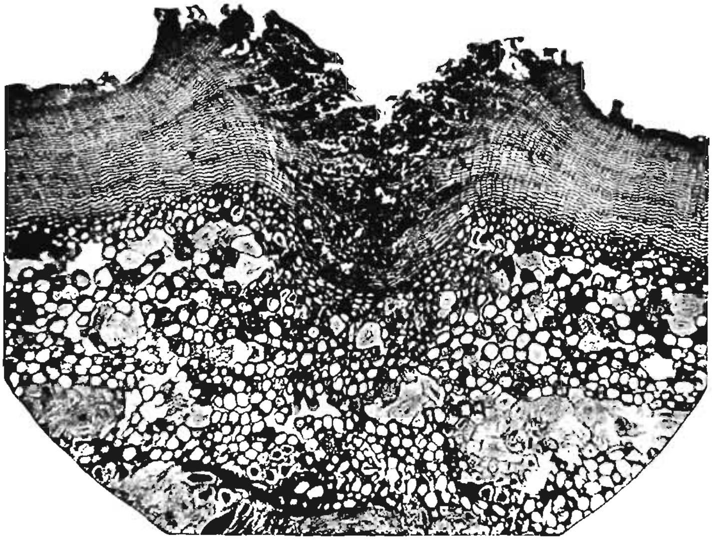


FIG. 55.—Cross section of a portion of the cortex and corky bark of a young stem of cherry, showing a lenticel. (*From Eames and MacDaniels.*)

Phloem.—The fibro-vascular cylinder is composed of two distinct tissues. On the outside is the *phloem,* the function of which is to transport the elaborated foods—the carbohydrates, fats, and proteins—from one part of the plant to another, especially from regions of manufacture to those of storage or consumption. The cells concerned in this process are the *sieve tubes* (Fig. 56), elongated living cells with thin cellulose walls, unique in their lack of a nucleus. They are elongated parallel to the main axis of the stem and their end walls (more rarely their sides) are provided with *sieve plates* or definite groups of small perforations. Through these perforations extend threads of cytoplasm from one cell to another, so that the living substance of each sieve tube is directly continuous with that of the adjacent ones, thus allowing materials to pass from cell to cell without diffusing through the cytoplasmic membranes. In the highest

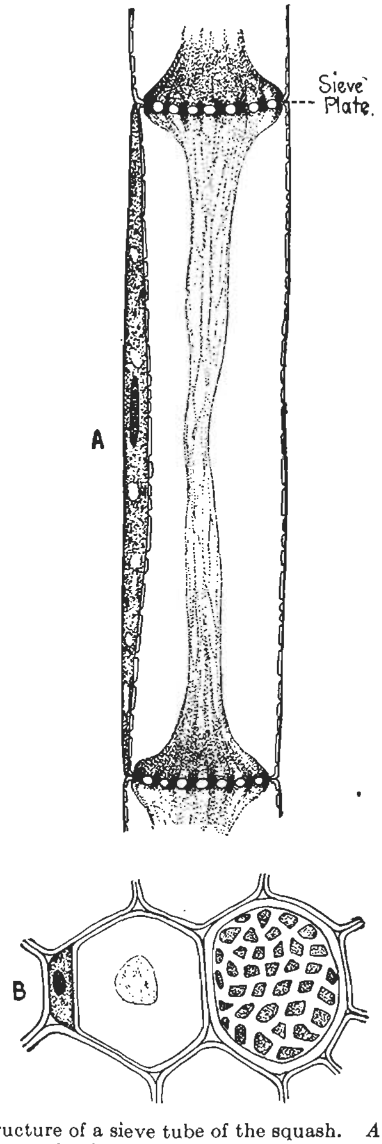


FIG. 56.—The structure of a sieve tube of the squash. *A*, longitudinal section of a sieve tube, communicating by sieve plates with the adjacent sieve tubes above and below. Its companion cell is at the left. *B*, transverse sections through two sieve tubes. The one at the left is cut near the middle; that at the right is cut near the end and shows the end wall or sieve plate.

seed plants there is adjacent to each sieve tube a small *companion cell*, provided with an abundance of cytoplasm and a nucleus. In addition to these two types, groups of long and very thick-walled cells, the *bast fibers*, serving as a mechanical protection for the thin-walled sieve tubes, characteristically occur in the phloem, and some parenchyma is usually present there also.

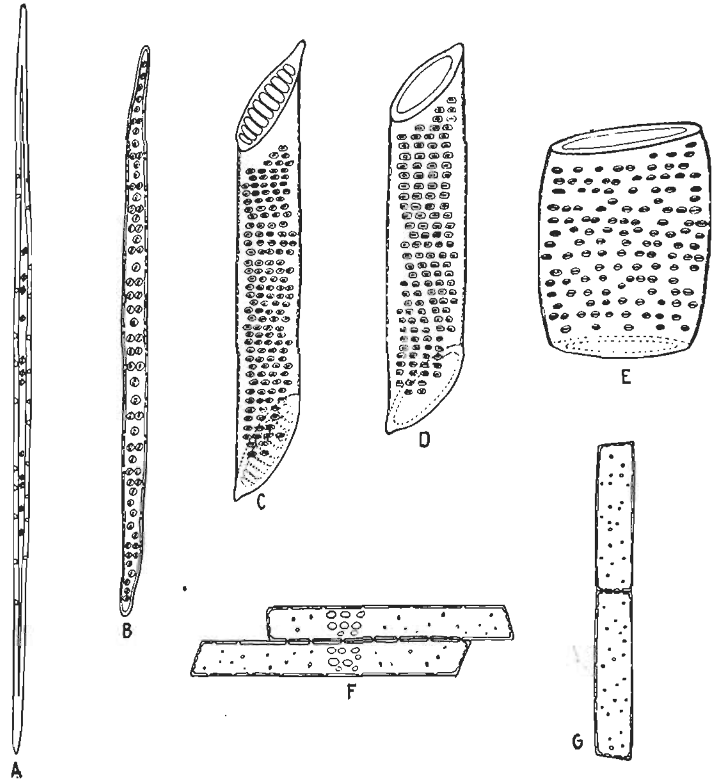


FIG. 57.—Types of cells found in wood. *A*, fiber; *B*, tracheid; *C*, vessel cell with ladder-like end wall; *D*, vessel cell with completely open or *porous* end wall; *E*, very short, broad, vessel cell; *F*, two ray cells; *G*, two vertical wood-parenchyma cells.

Xylem.—The inner portion of the fibro-vascular cylinder consists of the *wood* or *xylem*, which provides mechanical rigidity for the stem and transports the stream of water and dissolved substances from root to leaf. As essential elements in the xylem are found cells which are much elongated parallel to the main axis of the stem and in which the cellulose walls have become very thick and woody (Fig. 57, *A-E*). Such walls are said to

be *lignified.* As soon as one of these cells is fully developed, it dies and its protoplasmic contents disappears, so that only the thick, woody cell wall is left. Definite thin areas or *pits* occur at frequent intervals along this wall and facilitate the rapid movement of water. In simpler types of wood, such a cell is able to provide both the necessary rigidity and the conductive capacity and is known as a *tracheid.* In the higher types, however, this simple element has become specialized in two directions and has given rise to long and very heavy-walled cells, the *wood fibers,* in which almost no cavity remains and which contribute a high degree of mechanical strength to the wood; and the *vessel cells* or *tracheal cells,* much shorter, with wide cavities, and walls which are comparatively thin and are provided with large perforations in their ends. These cells, distributed end-to-end in vertical rows, constitute the *ducts* or *vessels,* so characteristic of the wood of many plants, which carry the ascending stream of water through the stem. Parenchyma cells sometimes occur among the lignified elements and like them may be elongated vertically (Fig. 57, *G*). Other parenchyma cells are elongated *at right angles* to the stem (Fig. 57, *F*) and dispersed among the woody cells in horizontal bands or ribbons running out through the xylem along the radii of the stem. These structures are known as the *wood rays,* and in somewhat modified form extend also into the phloem. They facilitate the horizontal transfer of materials in the stem and are of particular importance as centers of food storage.

Cambium.—A narrow layer of thin-walled cells, the *cambium,* separates the wood from the phloem. Through its activity new cells are added to the outside of the wood and the inside of the phloem, and the thickness of the stem thereby is increased. Among woody plants, such growth continues from year to year and each season's increment, an *annual ring,* is easily recognizable.

At each node a small but complete segment of the fibro-vascular ring separates from the rest and passes out through the cortex into the base of the petiole as a *leaf trace,* causing a break, or *leaf gap,* in the ring. Into each leaf may enter one, three, five, or more of these traces which are destined to pass upward through the petiole and to form the system of veins in the blade.

Woody and Herbaceous Stems.—The perennial woody stem in which the fibro-vascular cylinder, as seen in cross section, forms a continuous and rather wide ring (except for the leaf gaps), and

which receives additions in thickness year by year through cambial activity, is probably the most ancient stem type among seed plants; and the herbaceous condition, where the stems are much softer and shorter lived, has apparently been derived from it in response to climatic changes or for other reasons. In herbaceous species, the amount of fibro-vascular tissue is proportionally very much less. This may be due simply to a decrease in the activity of the entire cambium, or to the breaking up of the cylinder into separate bundles; but in general any

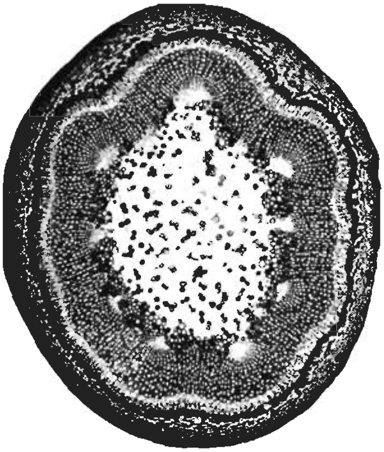


FIG. 58.—Transverse section of a one-year-old stem of the sweet gum (*Liquidambar*) showing the continuous fibro-vascular cylinder.

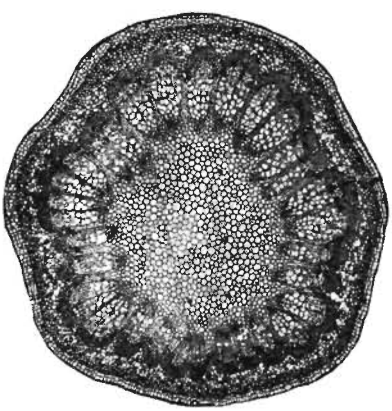


FIG. 59.—Transverse section of a one-year-old stem of the sycamore (*Platanus*) showing the fibro-vascular cylinder broken up into segments by the development of wide rays.

herbaceous stem is roughly comparable to a one-year-old twig of the particular woody stem-type from which it has been evolved. The herbaceous stem in Fig. 60, with its thin but continuous vascular ring, has probably arisen from some such woody form as is shown in Fig. 58, where the vascular ring is similarly continuous and homogeneous. The stem in Fig. 61, however, in which the cylinder has been broken into distinct and completely separate bundles, is quite different in type and has probably arisen from a woody stem somewhat resembling that in Fig. 59, where the vascular ring is divided into segments by the development of very wide rays. Cambial activity is usually weaker opposite these rays than opposite the woody segments of the cylinder, and in the stouter herbs of this type the rays therefore

tend to form broad constrictions in the ring. In more delicate herbaceous stems the constrictions finally become complete, the broad rays disappear, and the cylinder is thus broken up into a ring of separate segments or *fibro-vascular bundles*. Each of these consists of a group of wood cells on its inner side and of phloem cells on its outer, with a vestige of cambium between them. Connecting the cambium layers of two adjacent bundles there may be a weak *interfascicular* cambium, producing a few layers of parenchyma cells. In many herbaceous stems however, the

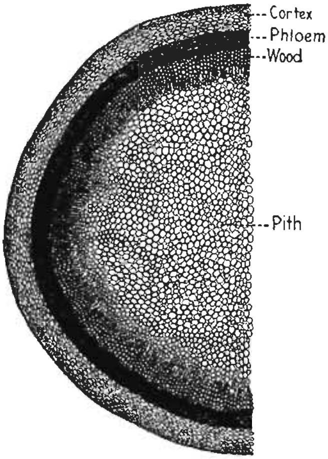


FIG. 60.

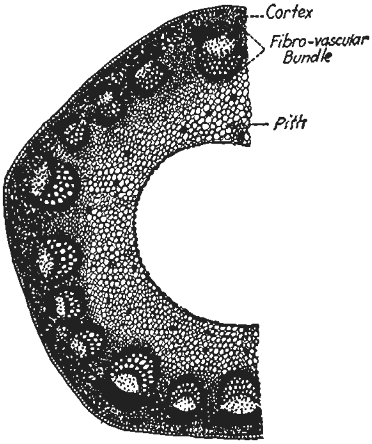


FIG. 61.

FIG. 60.—Transverse section of the stem of an herbaceous plant (*Digitalis*). In this type the fibro-vascular cylinder is thin but unbroken.

FIG. 61.—Transverse section of an herbaceous stem (*Delphinium*). In this type the fibro-vascular cylinder is broken into a ring of fibro-vascular bundles, each containing a group of wood cells and a group of phloem cells.

bundles, each surrounded by a *bundle sheath* of thick-walled cells, are quite distinct and widely separated from one another, with no remnant whatever of a cambial zone between them. It should be noted that in these bundles the phloem is directly outside the wood, and that the alternation of bundles of wood and phloem, characteristic of the vascular cylinder of the root, is absent in the stem.

The Stem of Monocotyledons.—Stems of this type (Fig. 62) are even more highly specialized than those of herbaceous dicotyledons. The bundles which constitute the fibro-vascular system here are entirely distinct from each other, and are no longer arranged in the form of a hollow tube but are scattered irregularly

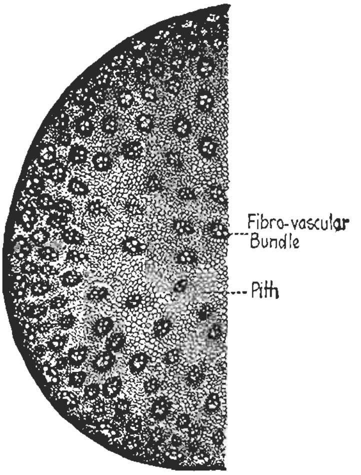


FIG. 62.—The stem of a monocotyledonous plant (corn). Transverse section, showing the fibro-vascular bundles scattered in the pith.

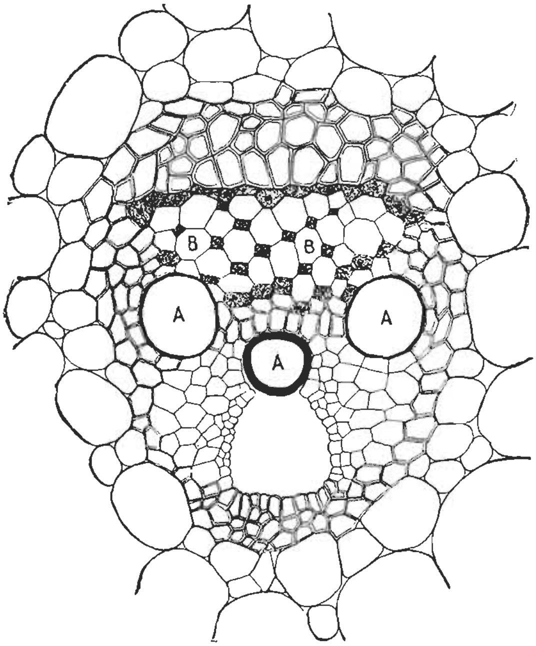


FIG. 63.—Stem bundles of a monocotyledonous plant. Transverse section of a fibro-vascular bundle from the corn stem shown in Fig. 62. *A*, vessels; *B*, sieve tubes, with companion cells in their corners. The bundle is surrounded by a *bundle sheath* of thick-walled cells.

throughout the whole area of the stem, although somewhat more abundantly toward the outside than toward the center. Pith and cortex are no longer sharply separated by a ring of vascular tissue, and it is impossible to distinguish the one from the other, the whole general ground-tissue of this type of stem being called the pith. The individual bundles are distinctive in appearance, and the corn bundle in Fig. 63 is typical of most of them. Around it, as in other herbaceous bundles, is a bundle sheath of thick-walled cells. The xylem portion of the strand, which ordinarily is on the side toward the center of the stem, consists chiefly of two very large ducts. Between these is a narrow band of wood cells, and below this a large air space or *lacuna,* a portion of which is occupied by a vessel with ring-like thickenings in its walls. The phloem is regularly arranged, the eight-sided sieve tubes alternating with rectangular companion cells. The departure of the strands to the leaves is very complex, a large number of bundles moving outward from the stem and entering the sheathing leaf base.

The Structure of Wood.—In shrubs and trees* the great bulk of the stem, particularly in its older portions, consists of but one tissue, the wood. Wood is so important in the economy of the plant and of such great significance to man that it perhaps deserves a closer study than has been given the other tissues of the stem.

Through the activity of the cambium (a fuller account of which is reserved for the chapter on growth) a new concentric layer of wood cells is added each year to the outside of the woody cylinder. The tracheids and ducts produced at the beginning of growth in the spring are usually of large diameter and are accompanied by comparatively few fibers, and it is apparently in this *spring wood* that most of the upward conduction of water takes place. In the later-formed portion of the annual ring, the water-carrying cells are fewer and narrower, and the bulk of the tissue is composed of fibers. This *summer wood* is responsible for most of the rigidity and strength of the stem. In large branches and trunks, the older portion of the wood, consisting of the first-formed annual rings at the center of the stem, in time becomes dead throughout and ceases to perform its functions of water conduction and storage. It then constitutes the *heart wood* (Fig. 64)

* Conifers and dicotyledons alone are discussed here. Woody monocotyledons are rare and their vascular tissues are very complex.

and frequently is distinguished from the outer layers by its darker color. The living and functioning part of the wood is its youngest portion and is known as the *sap wood* (Fig. 64). This, of course, is on the outside of the woody cylinder, and it is usually rather constant in width in any particular species, its innermost ring being converted into heart wood each year as its outermost is added by the activity of the cambium. All of the non-woody cells in the sapwood (the parenchyma cells and ray cells) are alive. The ducts in heart wood are often plugged up

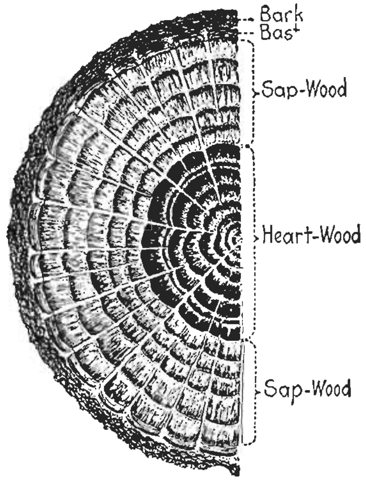


FIG. 64.—Heart wood and sap wood. Transversely cut end of an oak log showing the darkly colored heart wood at the center of the stem, surrounded by the lighter sap wood.

by balloon-like ingrowths, or *tyloses*, from the adjacent parenchyma cells.

Wood usually is cut along one of three distinct planes, and the cut surface in each case presents a very different appearance (Fig. 65). In describing a given wood it is therefore customary to consider its characteristics as they are shown in these the cuts or *sections*. An ordinary "cross cut," at right angles to the length of the log, is known as a *transverse* section, and shows the annual rings as a series of concentric circles, with the wood rays running out from the center as narrow lines along the radii. Where the cut is longitudinal and made exactly along the radius of the log, a *radial* section results. This presents the

annual rings as vertical straight lines and the wood rays as horizontal stripes or markings. Where the rays are fairly wide, as in the oak, these markings are prominent and furnish the much-prized "silver grain" so readily seen in quartered oak. Other longitudinal sections, which do not lie in a plane passing through the center of the log, are known as *tangential*. If the structure is exactly regular and the cut exactly true, the annual rings are here seen as straight lines somewhat unequally distant, running up and down along the wood. The irregularities which almost

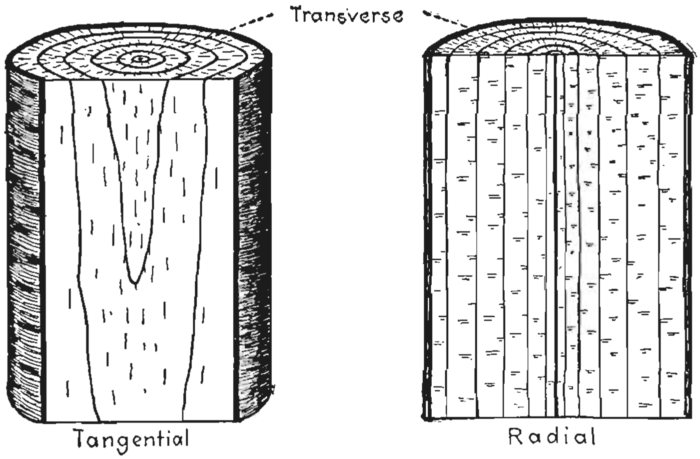


FIG. 65.—Transverse, tangential, and radial sections of wood. Both logs have been cut transversely. The one at the left has also been cut lengthwise tangentially, and the one at the right lengthwise radially. Each cut represents the appearance of that particular plane of section. The annual rings and wood rays may be distinguished in all three sections.

always occur, however, cause the rings in such a cut to appear as wavy lines which produce the common "grain" of most wood surfaces. The rays are very inconspicuous in a tangential section, for only their cut ends are visible. The relations between these three sections, and the characteristic appearance of the various wood structures as seen in them, are shown in the segment of an oak log (Fig. 66) and the magnified cube of pine wood (Fig. 67).

Woods of various species differ from one another markedly in such gross characters as color, weight, hardness, chemical composition, width of annual rings, width of rays, and number, size and arrangement of vessels; and in such microscopic features as the size, shape, character, and location of the different classes of

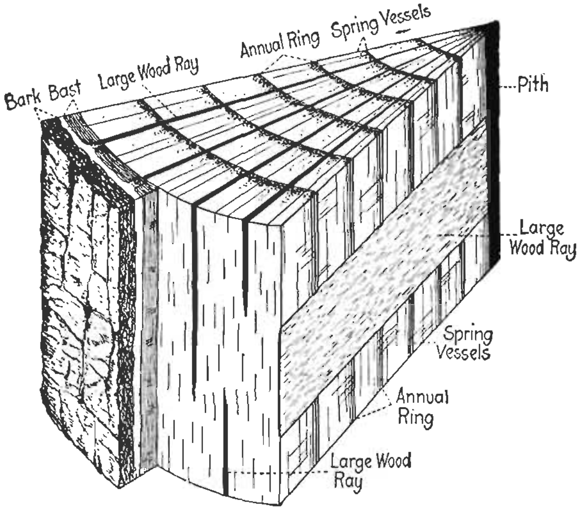


FIG. 66.—A segment of an oak log. At the right, the block has been cut radially; and above, transversely. At the left (the surface of the log) a portion of the phloem and bark has been removed, showing a tangential view of the wood underneath. The wood rays are narrow sheets of tissue running along the radii of the stem. On the radial face one of them is shown split open, giving the characteristic "silver grain" of oak wood. Between the large rays are many small and narrow ones.

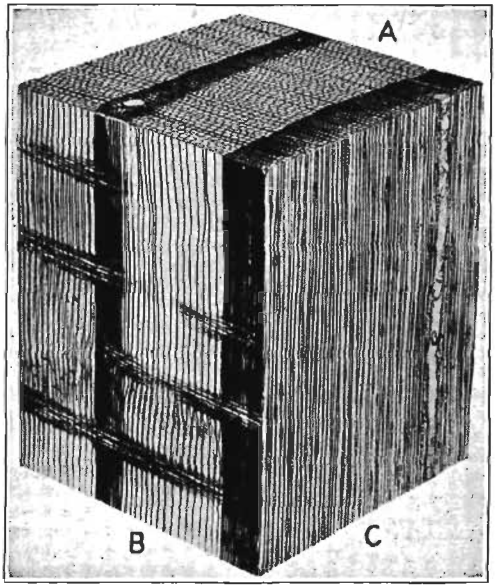
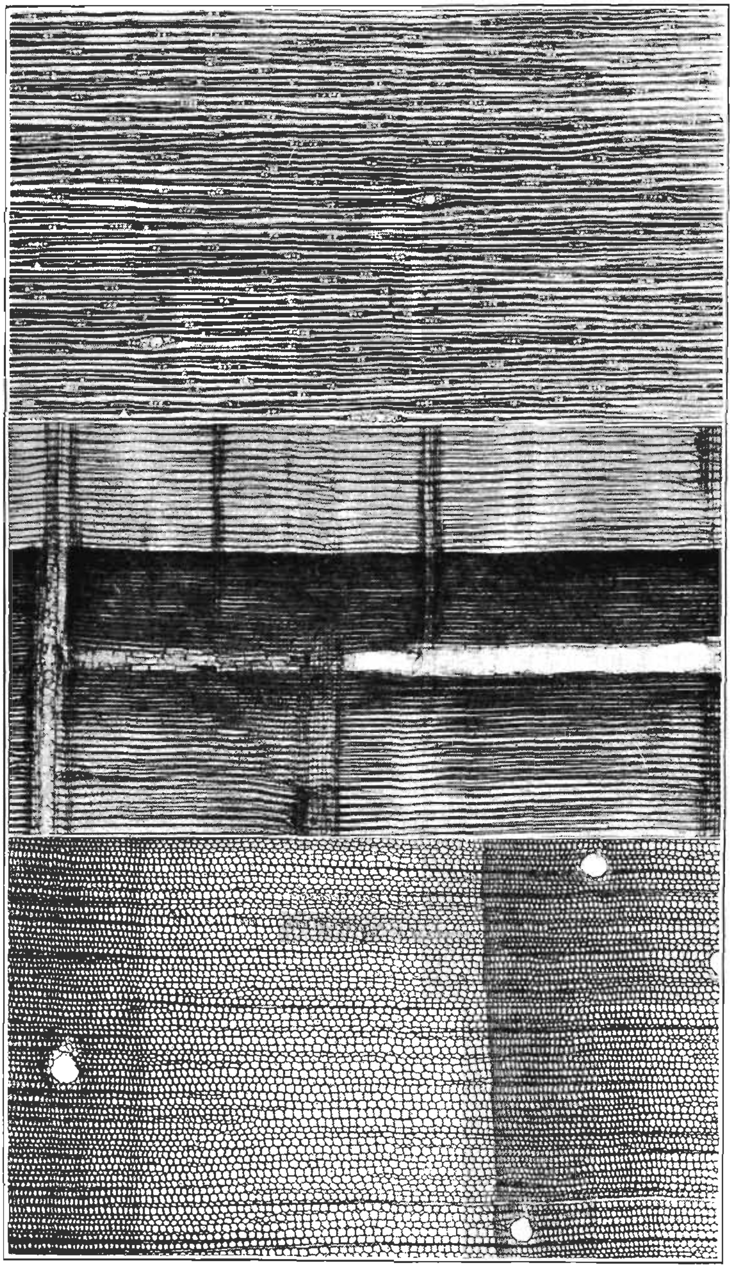


FIG. 67.—Cube of pine wood, much enlarged. *A*, transverse section; *B*, radial section; *C*, tangential section. One entire annual ring and parts of two others are shown. (*Courtesy United States Forest Products Laboratory.*)



A *B* *C*

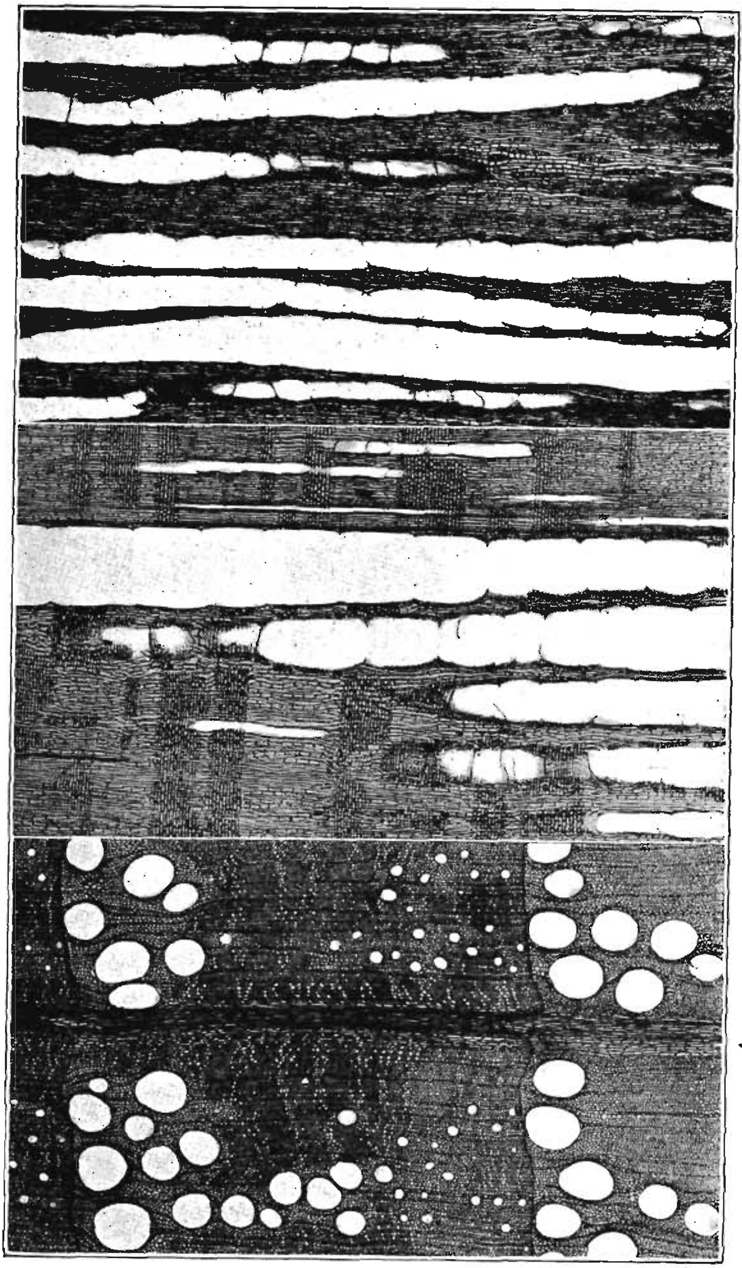
Fig. 68.

wood elements, the type and distribution of pits, and the various markings on the cell walls. The structure of two distinct and important woods, those of pine and of oak, are well shown in their transverse, radial, and tangential sections in Figs. 68 and 69. The various details of wood structure remain so constant that they often may be used to identify the plant species from which a piece of wood has been derived. The great diversity which wood displays, together with its abundance and the ease with which it can be manipulated, have led to its use in numberless ways, and there is consequently no other plant tissue, aside from those used as food, which is of such great economic importance.

Storage and Secretion in the Stem.—The function of the stem as a center of food storage has already been mentioned. It is chiefly in its perennial portions, both subterranean and aerial, that reserve food is laid down, although there is some temporary deposition in annual stems. Any living cells may function in food storage, but the pith, the cortex, and the wood and phloem parenchyma (particularly the parenchyma of the rays) are chiefly concerned. Starch is the commonest type of food stored, though fats and proteins are often found.

In the cortex and wood of the stems of many coniferous trees there occur specialized canals which secrete resin or "pitch." The formation of these canals can be stimulated by wounding the stem and the secretion, in the case of many pines, is commercially important as the basis of turpentine and its products. Oil, mucilage, and tannin are also secreted by canals or specialized cells in various parts of the stems of many plants. Still more important today, from its use in the manufacture of rubber, is *latex*, a remarkable milky secretion found in the milkweed, the dandelion, the fig, and various rubber-producing plants. This material is secreted in a complex system of branching tubes often extending throughout the stem, and especially developed in the bark.

FIG. 68.—Pine wood as seen under the microscope. *A*, transverse section. The wood cells (tracheids) are here cut across, at right angles to their length. Note the thin-walled cells in the spring wood and the thick-walled ones in the summer wood. The wood rays run at right angles to the annual rings. *B*, radial section. *C*, tangential section. In both these, the tracheids are cut lengthwise. Note the marked difference in the appearance of the wood rays in the three sections. The large openings are resin canals. (*Courtesy United States Forest Products Laboratory.*)



C B A

Fig. 69.

Modified Stems.—The typical upright, foliage-bearing stem has sometimes become radically modified. Many plants have abandoned the erect habit, and their weak and slender stems are prostrate on the ground (Fig. 70) and often strike root there. Some climb on or twine about other objects, and thus are able to expose their leaves to the light without developing a stout stem.

FIG. 70.—Prostrate stem of the twin-flower (*Linnæa*). (*From Ramaley.*)

Still others, such as the carrot and the dandelion, produce little or no stem, at least during certain stages of their life history. In certain perennial herbs the main stem has become subterranean and serves chiefly for food storage, sending up leaves or shoots to the surface. Rather slender underground stems of this sort are known as *rootstocks* or *rhizomes* (Fig. 71). In extreme cases they have lost their power of foliage production altogether, and have become shortened and much thickened into *tubers* (Fig. 72), as in the potato plant. Here the foliage leaves

FIG. 69.—Oak wood as seen under the microscope. *A*, *transverse section*, showing one complete annual ring and parts of two others. Note the very wide vessels in the spring wood, the narrow ones in the summer wood, the wide wood ray, and the many very narrow ones. *B*, radial section. *C*, tangential section. Note the many differences in structure between this wood and that of pine. (*Courtesy United States Forest Products Laboratory.*)

are borne on typical aerial shoots, and the fact that the tuber *is morphologically a stem is indicated only by its structure.*

Other stems modified for food storage (Fig. 73) are the *bulb* (as in the onion), which consists of a much shortened stem bearing

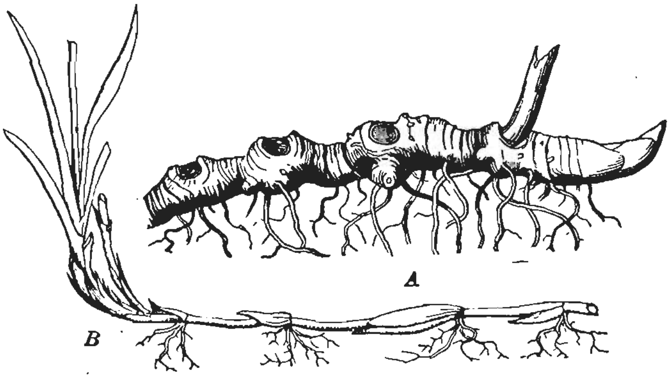


FIG. 71.—Rootstocks. *A*, slender rootstock of sedge, showing the reduced leaves on the underground portion of the stem, and the origin of roots at the nodes. *B*, stouter rootstock of Solomon's seal. (*After Gray.*)

a cluster of thick and fleshy leaf bases; and the *corm* (as in the crocus), where all the food is deposited in the short, stout stem itself.

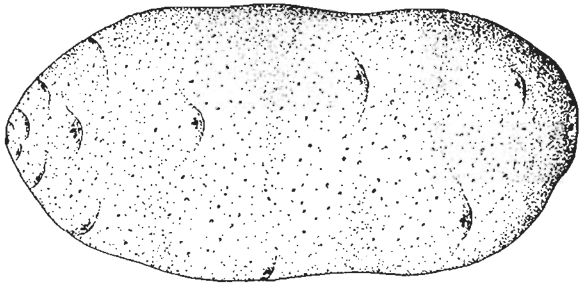


FIG. 72.—Tuber of the potato, showing point of attachment to the parent plant (at extreme right) and numerous buds or "eyes," each in the axil of a reduced and scale-like leaf.

Many stems, particularly the prostrate ones and the rootstocks, are of much importance to the plant in effecting its distribution and in producing new individuals by vegetative means. The use of strawberry "runners" and potato tubers in the

propagation of these plants is familiar, and will be discussed more fully in the chapter on reproduction.

The Ascent of Sap in Stems.—It can be determined by experiment that water and dissolved substances absorbed by the roots are carried upward in the wood of the stem. As to what causes this movement, however, there still is much question. To

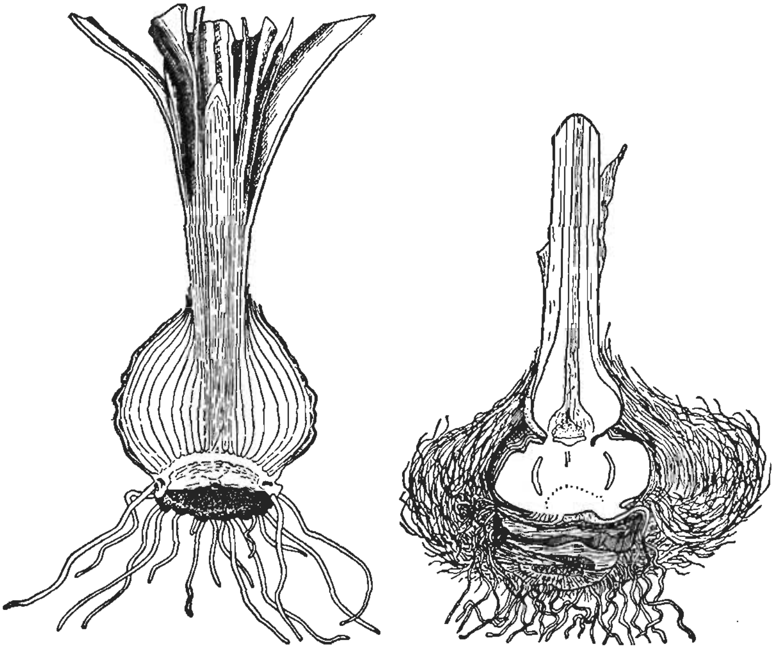


FIG. 73.—Bulb and corm. At left, longitudinal section through the bulb of a hyacinth. The short, broad stem bears a cluster of fleshy leaves, the central ones of which grow out as foliage leaves. At right, longitudinal section through the corm of a crocus, showing the thick, short stem surrounded by the fibrous remains of old leaf-bases. The remains of corms of three preceding seasons are *shown below the present one. The tops of the leaves have been cut off in both* illustrations.

explain the ascent of water in low-growing herbaceous plants is fairly simple, but the factors which bring about the lifting of water in large quantities to the tops of tall trees, sometimes more than three hundred feet above the ground, are very hard to determine. An upward osmotic pull is of course furnished by the increased sap concentration in the leaf cells which follows the water loss therefrom in transpiration, or by the force of imbibition in the drying cell walls; but even granting a strong pull at the leaf, the rise obviously cannot be due to simple "suc-

tion" or atmospheric pressure. Nor is capillarity probably concerned to any great extent in the process, for, although water may be lifted very high in exceedingly small capillary tubes, its movement is so slow under these conditions that capillarity certainly could not provide the large amounts of water which must ascend the trunk daily. Root-pressure, if it were great enough, might perhaps be important, but root-pressure is strongly manifest in most woody plants only during the spring and therefore is lacking at the season when transpiration is most active. It has been suggested that the living ray and wood-parenchyma cells may be concerned in the upward movement of water in some way, perhaps furnishing a continuous series of osmotic pumps. These cells may be of some such service, but it has been shown that for a considerable time, at any rate, water may ascend through a stem where all the living cells have been killed. The most plausible hypothesis yet put forward is based on the very high cohesive power exhibited by water under certain conditions. In thin water columns, such as occur in the conducting cells of the wood, this cohesive power apparently is so strong that a pull at the top—in this case the osmotic pull in the leaf cells—will lift a very tall water column bodily, as a rope might be lifted. There are certain objections to this explanation, too, but they are not as serious as in the other hypotheses. Possibly several of the factors mentioned may be concerned together in the ascent of sap. It must be admitted that this problem, like so many others in biology, has not as yet reached a satisfactory solution.

The Translocation of Foods.—The plant must possess means not only for insuring the passage of a plentiful supply of water to the leaves through the wood of the stem, petioles, and veins, but also for transporting the product of leaf activity—the manufactured food in the form of simple carbohydrates, fats, and proteins—to any region of the plant where food is used or stored. This function of translocation is performed chiefly by the sieve tubes of the phloem. The movement of organic substances by diffusion from cell to cell is a comparatively slow process, but is the only means available in regions remote from the vascular system. Movement of food for long distances, as from the leaf to the storage regions of stem and root, seems to take place chiefly in the phloem. As to just how this translocation is brought about, however, uncertainty still exists, although there is

evidence that the streaming of living substance in the phloem cells is a factor. The importance of the phloem has repeatedly been demonstrated by experiments involving "ringing" or "girdling," in which there has been removed from around the stem a continuous encircling strip of tissue, including all bark and phloem. It is a matter of common observation that a tree in which the trunk has been girdled in this way will ultimately die. Although small in amount, therefore, and rather inconspicuous when compared with the wood, the phloem is a vitally necessary tissue in the economy of the plant.

QUESTIONS FOR THOUGHT AND DISCUSSION

271. Most stems tend to be stout below and more slender above. Why is this, and of what advantage is it to the plant?

272. Why are young trees often somewhat spire-shaped, but old trees of the same species rather flat or convex at the top?

273. What difference in method of stem growth is responsible for the differences in shape between a spruce tree and an elm tree?

274. What advantages and what disadvantages does a climbing plant have as compared with an erect one?

275. What advantages and what disadvantages does a plant with a prostrate stem have as compared with an erect one?

276. What advantages and what disadvantages does an herbaceous plant have as compared with a tree?

277. Why are the stems of submersed water plants soft and weak?

278. Give an example of a plant which is practically stemless.

279. By looking at a leafy branch which has been freshly cut from a tree, how can you tell whether it has been growing in a vertical, horizontal, or oblique position there?

280. Will all the buds present on a tree in the winter unfold and grow into branches the next spring? Explain.

281. What functions do you think that the bud scales perform? Which is probably the most important of these functions? Explain.

282. The scale of a winter bud and the flap of skin below the "eye" of a potato are both said to be "modified," "reduced," or "vestigial" leaves. Why are they regarded as leaves at all, and what has probably been their history?

283. Why is a potato "morphologically" a stem?

284. Why is it that a woody twig obtains air for its internal tissues through lenticels rather than through stomata, as does a leaf?

285. What is there about the structure of cork which makes it such excellent material for bottle stoppers?

286. What is meant by the statement that the cortex and pith are "undifferentiated" tissues?

287. What advantage is there in having the cells of the conducting tissues much elongated?

288. Wood has a "grain" which generally runs parallel to the axis of the tree. To what is this grain due?

289. Why does wood split easily "with the grain" but not "against the grain?"

290. What causes knots in wood?

291. Why does a log which is otherwise free from knots often show them near its center?

292. Which will have more and larger knots in its wood, a tree grown in the forest or one grown in the open? Explain.

293. Why is the wood of a knot harder than the surrounding wood?

294. By looking at the cut end of a board, how can you tell the position which this board held with reference to the center of the log from which the board was cut?

295. How can you tell whether a piece of furniture is made of veneered wood or not?

296. In what two ways can you tell the age of a twig?

297. What makes the annual rings in wood clearly distinct from one another?

298. Why is it often difficult to count the annual rings of trees which have grown in warm regions?

299. As a tree grows older, which increases more rapidly in thickness, its heart wood or its sap wood? Explain.

300. Which will decay faster if exposed freely to the air, heart wood or sap wood? Explain.

301. In most woody plants it is only the least year's growth of phloem, or at most that of the last few years, which functions in translocating food. Explain.

302. What do you think is the chief function of the bast fibers?

303. What do you think is the function of the companion cells?

304. How would you determine whether or not the ascending stream of water travels in the wood?

305. Why cannot the ascent of water in the stem of a plant be explained on the principle of the suction pump?

306. Species of trees differ markedly in the height to which they can grow. What factor may be responsible for these differences?

307. The vessels in the wood of vine stems are usually much wider than those in the wood of trees. Explain.

308. It has been found that the osmotic concentration of the sap in the leaf cells increases steadily from the lower leaves to the upper ones on a tree. Explain.

309. How is it possible for a tree which is "hollow hearted" to thrive and grow?

310. In tapping maple trees for sap, why is it necessary to run the tap into the tree for only a very short distance?

311. Cut flowers will keep fresh longer if the cut ends of their stems are trimmed off daily; if, after cutting, the ends are placed in boiling water or a flame for a moment; or (sometimes) if a little salt is added to the water. Explain how it is that these various procedures tend to effect the desired result.

312. Why will a girdled tree ultimately die?

313. Why is the chestnut-bark disease, which attacks only the outer bark, cortex, and phloem, so fatal to chestnut trees?

314. Why is a wire ring or other tight metal band around a tree trunk likely to injure the tree severely in time?

315. If a trunk is bound tightly with wire, a swelling of the tissues finally appears above the wire. Explain.

316. In propagating a plant by "layering," a gardener bends a branch down to the ground and covers a portion of it with earth in order that it may root at that point. Roots will develop much faster if the stem is bent or twisted strongly at the point where the roots are desired. Explain.

317. In "Chinese" layering, a ring of bark is cut off around the stem as far in as the wood, and that part of the stem is covered with moist moss. Roots eventually appear above the ring but not below it. Explain.

318. In order to obtain very large fruits for exhibition purposes, growers sometimes "ring" a fruit-bearing branch some distance below where the fruit is growing. Explain why this has the desired result.

319. What foundation in fact is there for the old belief that by driving nails into the trunk of a plum or peach tree, larger fruit will be obtained?

320. If a tree is girdled while its leaves are out, would you predict that the leaves would wilt or not?

REFERENCE PROBLEMS

66. Give an example of a stem which has assumed some of the functions of a leaf; of a root; of a reproductive organ.

67. Make as complete a classification of buds as you can.

68. Give an example of a plant in which the bud scale is a modified leaf blade; of one in which it is a modified petiole; and of one in which it is a pair of stipules.

69. Describe and name the various ways in which the young leaves may be folded in the bud (their *vernation*); and the various ways in which the floral structures may be folded there (their *aestivation*).

70. Why does a gardener use "brush" to support peas but poles to support beans?

71. Why do apple and elm trunks make better chopping blocks than do most woods?

72. What is the essential feature in the manufacture of wood pulp? Why is paper made from wood pulp so much less tough than that made from cotton or linen?

73. What anatomical differences distinguish the wood of conifers from that of "broad-leaved" trees (angiosperms)?

74. What is the difference between a wood which is *ring porous* and one which is *diffuse porous?* Give a common example of each.

75. Of what advantage to the plant are the tyloses which sometimes occur in heart-wood?

76. What is "quartered oak?" Why is it more expensive than ordinary oak? Why can oak be quartered to advantage whereas most woods cannot?

77. Give an account of the sources and methods of production of crude rubber.

78. Give the author and title of three important books dealing with the structure or functions of the stem, and outline briefly the content of each.

79. Name several botanical investigators who have done important work on wood structure or on the movement of sap in stems, and state the notable contributions made by each.

80. Give the derivation of the following terms and explain in what way each is appropriate:

Node	Cortex	Lenticel
Xylem	Tracheid	Phyllotaxy
Phloem	Cambium	Fibro-vascular

CHAPTER VII

METABOLISM

The term *metabolism*, whether used of animals or of plants, refers to the entire series of chemical changes and processes involved in the activity of the living organism. It may be divided roughly into *constructive* and *destructive* metabolism. The former process begins, in plants, with the production of simple carbohydrates by photosynthesis, and is concerned with the construction from these of the more complex plant foods and with their storage, digestion, and assimilation into the living protoplasm, together with the growth of new tissues which is thus made possible. Destructive metabolism involves a breaking down of protoplasm and its inclusions, with the consequent production of waste materials and the liberation of energy necessary for the activity of the living organism.

Plant Foods.—Before the characteristics of these various food types and their mode of origin are considered, however, one should inquire as to just what is implied by the term *food* itself. A broad definition makes food include everything taken into the body of the organism which is essential to its life and continued activity. Water, carbon dioxide, and the various essential mineral salts would thus be considered as the food of plants; and indeed it is the last of these which in ordinary speech are most commonly referred to as "plant foods." From such a conception of food as this, however, has arisen a fallacious distinction sometimes drawn between animals and plants, namely that the former require organic food and the latter only inorganic. A more strict and from the present point of view a more useful employment of the term food limits its application to anything which supplies either of the two fundamental needs of the organism—energy and building materials. Food may therefore be defined as *whatever furnishes a supply of available energy to an organism or contributes materially to the upbuilding of its tissues*. It is the carbohydrates, fats, and proteins which provide the materials for growth, and which, because of their somewhat

unstable chemical composition, contain a supply of potential energy readily available to the organism. These are the true foods. The essential mineral salts, which constitute a very small portion indeed of the plant body, are neither tissue builders (except in a very minor degree) nor energy producers, and hence cannot strictly be regarded as plant foods at all. Their importance lies rather in the fact that they are necessary, in minute quantities, to the construction and successful functioning of

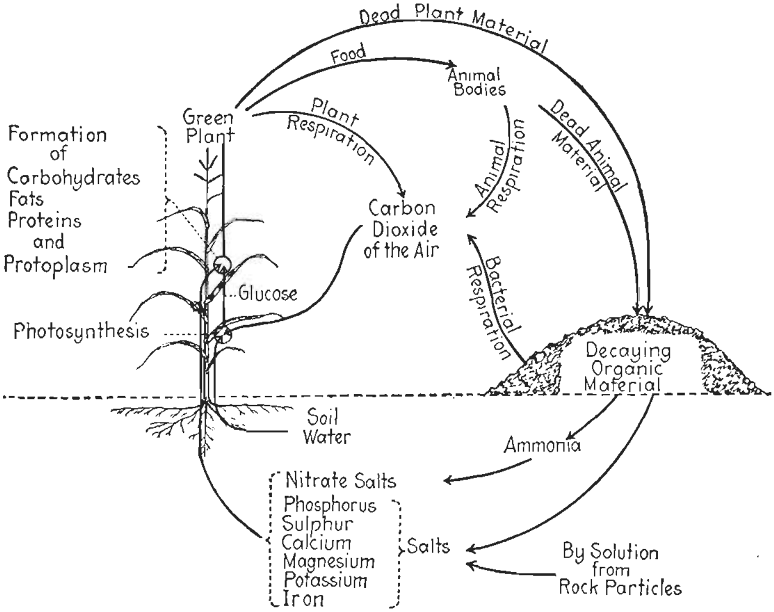


FIG. 74.—The organic cycle. History of the construction and disintegration of the important organic substances found in plants.

protoplasm itself. Together with water and carbon dioxide they may appropriately be called *nutrient materials*.

The food of plants and animals is essentially the same and the difference between the two groups therefore lies not in the character of the food which they use but in the fact that green plants are capable of synthesizing food from inorganic nutrient materials and that animals are not.

Given a simple food like glucose, however, plants are able to construct therefrom a great variety of more complex foods and of other organic compounds, and the animals which eat plants make still further changes in these food substances. There is

thus a constant circulation of various materials through air and soil and through the bodies of green plants, of animals, and of bacteria, a process by which organic substances are continually being built up and broken down. This *Organic Cycle* is represented graphically in Fig. 74.

Foods may be divided into three main classes: *carbohydrates, fats*, and *proteins*. These food types differ from each other in physical structure and chemical composition as well as in the parts which they play in nutrition.

Carbohydrates.—Carbohydrates are substances composed entirely of carbon, hydrogen, and oxygen, in which the hydrogen atoms are about twice as numerous as those of oxygen. Glucose ($C_6H_{12}O_6$), the product of photosynthesis, is an example of a very simple carbohydrate. To this group of foods belong the various sugars, starches, and celluloses. Carbohydrates are the chief source of energy for all organisms and also provide most of the building material for the plant body.

The *sugars* are soluble carbohydrates. Three are more common in plants than others. These are *glucose* or grape sugar, $C_6H_{12}O_6$, the direct product of photosynthesis; *fructose* or fruit sugar, identical in chemical formula with glucose but differing in the arrangement of its atoms and in certain physical characteristics; and *sucrose* (cane sugar or beet sugar), with the formula $C_{12}H_{22}O_{11}$, and produced from the simpler sugars by the removal of a molecule of water, thus:

$$\underset{\text{Grape sugar}}{2C_6H_{12}O_6} - \underset{\text{Water}}{H_2O} = \underset{\text{Sucrose}}{C_{12}H_{22}O_{11}}$$

These three types of sugar are all common in plants, though in any particular species one is usually more abundant than the others. Glucose and fructose form the bulk of the sugar of fruits and of the nectar of flowers, from which honey is derived, and are common elsewhere, glucose probably occurring in every living plant cell. Sucrose is abundant in the sugar cane and sugar beet and is therefore the type of sugar most used as human food. Sugars are stored in some plants as reserve foods, but are also widely distributed in small quantities throughout the plant body because of the fact that those carbohydrates which are insoluble must be converted into sugar before they can be transported from place to place, or before they can be assimilated into living protoplasm.

The *starches* are insoluble carbohydrates, derived from glucose but much more complex in their chemical composition. Their general formula is $(C_6H_{10}O_5)n$. Starch is produced from glucose by the removal of water, thus:

$$\underset{\text{Glucose}}{nC_6H_{12}O_6} - \underset{\text{Water}}{nH_2O} = \underset{\text{Starch}}{(C_6H_{10}O_5)n}$$

The formation of starch is confined to certain plastids in the cell. These are the chloroplasts, in cells where photosynthesis is going on, and the *leucoplasts* in storage cells. In these plastids the starch is laid down in small grains which increase in number and size until, in storage tissues, the entire cell cavity may

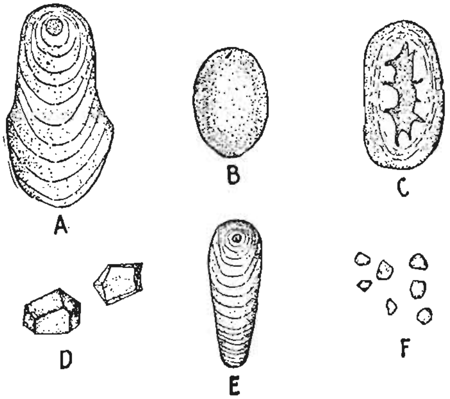


FIG. 75.—Starch grains from various plants. *A*, potato; *B*, wheat; *C*, bean; *D* corn; *E*, gloxinia; *F*, rice.

become filled with them. Starch grains usually display very characteristic shapes and markings distinctive of the species by which they are produced (Fig. 75). Indeed, it often is possible by this means to identify with certainty the source from which a particular sample of starch has been derived. A definite core or *hilum*, often cracked and shrunken, usually appears in the grain and is often surrounded by a series of more or less concentric rings or striations.

Cellulose is a carbohydrate even more complex chemically and physically than starch but with the same basic formula, $(C_6H_{10}O_5)n$. Because of its comparative indigestibility cellulose is not usually available as a food, though in certain plants a layer of it is deposited on the inside of the cell wall during periods of food storage and is later absorbed and used by the

plant. Such *reserve cellulose* is in some cases an important source of food. Of far more significance than its use as a food, however, is the fact that cellulose is the material out of which the cell wall, and therefore the entire skeleton of the plant, is constructed.

Fats.—Fats resemble carbohydrates in being composed only of carbon, hydrogen, and oxygen, but differ from them in the relative proportion of these elements. The hydrogen atoms are approximately twice as numerous as those of carbon, but in comparison with these two the amount of oxygen is very small. Three common plant fats well illustrate the chemical composition of this type of food. These are palmitin, $C_3H_5(CO_2C_{15}H_{31})_3$; stearin, $C_3H_5(CO_2C_{17}H_{35})_3$; and olein, $C_3H_5(CO_2C_{17}H_{33})_3$. Some fats are liquid and others solid at ordinary temperatures. Fats are insoluble in water and when moved about from cell to cell by diffusion a fat must therefore be broken down into its simpler and soluble components, chiefly fatty acids. In nature, fats are readily converted into sugars and sugars into fats. Fats are not as common a type of food as carbohydrates among plants, but nevertheless are of frequent occurrence in certain situations, particularly in seeds and other regions where food in concentrated form is advantageous. They apparently are not produced by any special plastids but appear in the form of minute droplets in the cytoplasm. Fats are important chiefly as sources of energy.

Proteins.—Proteins are composed not only of the basic carbon, hydrogen, and oxygen of the carbohydrates and fats, but include nitrogen also, and generally a small amount of sulphur. They are exceedingly variable, both in chemical composition and in physical properties, and are often very unstable. Protein molecules are large and enormously complex, as is illustrated by the calculated formulas of two common plant proteins, *zein* of corn, $C_{736}H_{1161}N_{184}O_{208}S_3$; and gliadin of wheat, $C_{685}H_{1068}N_{196}O_{211}S_5$. Less is known about proteins than about any other class of organic compounds. They are of particular interest from the fact that protoplasm itself is a mixture of complex proteins.

Proteins undoubtedly are formed by the union of a simple carbohydrate, such as the glucose which has been produced in photosynthesis, with nitrogen and sulphur which have been taken into the plant from the soil through the root hairs. This

union probably occurs most commonly in the leaves. It is a noteworthy fact that (with a few exceptions) plants alone seem to possess the ability to bring about this synthesis of protein, an ability almost as significant to the rest of the organic world as is that which enables them to manufacture carbohydrates from inorganic substances. Animals depend almost entirely upon plants for their supply of proteins. If given simple protein compounds, however, animals can build therefrom new and characteristic protein materials of all kinds.

Proteins, with their highly complex molecules, are not produced directly, but are built up by an aggregation of simpler nitrogenous compounds, the *amino acids*, which have been called their "building stones." Over twenty of these compounds have been isolated and studied. Among these are *glycine*, $C_2H_5NO_2$; *leucine*, $C_6H_{13}NO_2$; *glutamic acid*, $C_5H_9NO_4$; and *tryptophane*, $C_{11}H_{12}N_2O_2$. From these amino acids, with the addition of sulphur, are constructed all the proteins in almost infinite variety —the *albumins*, *globulins*, *prolamins*, and many others, which differ in composition, solubility, stability, and other respects.

Most of the protein which is stored as a reserve food in plants occurs in definite bodies, the *aleurone grains*, which are secreted by the protoplasm much as are starch grains, and which often fill the sap cavity. The storage of proteins in this form is frequently confined to particular regions of the plant. Thus the *aleurone layer* of cereal grains, a single layer of cells just under the pericarp, is filled with aleurone and is thus rich in protein.

Proteins are much less abundant as reserve foods than are carbohydrates, and are relatively poor energy producers, but their composition makes them far more effective than any other foods in the construction and renewal of living substance. As "tissue builders" proteins therefore play a vital part in the nutrition of plants and animals.

Digestion.—It has already been pointed out that the physiological processes of a plant are concerned almost entirely with substances which are in *solution*, and that in order to enter the plant body from the soil or the air or to pass from one cell to another within it, a substance must first be dissolved. Insoluble materials are of little immediate significance in the economy of protoplasm. Most of the food substances which have just been discussed exist commonly in forms which are not soluble in water. The advantages of this in the storage of reserve foods is

obvious. It is evident, however, that before such foods can be moved or *translocated* within the plant, and before they can be assimilated into living protoplasm, they must in some way be made soluble; and it is this process of converting an insoluble food into soluble form which is known as *digestion*.

Digestion is brought about through the activity of certain highly important but little understood substances known as *enzymes* or *ferments*. Enzymes are concerned not alone in digestion but in the production of many other chemical changes in the plant. They occur in great variety and probably are protein in character, although their composition is not definitely known. Enzymes are usually present in exceedingly small quantities but are able to effect profound chemical changes out of all proportion to their bulk. How they do this is not understood. The enzyme apparently does not enter into the composition of the substance produced, nor does it contribute energy for the process, and it is not consumed or used up. It seems merely to hasten a chemical reaction which might still take place, very slowly, in its absence. Enzymes have thus been said to "lubricate" reactions. Temperature largely controls their rate of activity, each enzyme having an optimum temperature at which it works most rapidly. These remarkable substances may be destroyed by heat and even by certain poisons. Aside from effecting digestion, they are concerned with the changes which take place in the various fermentations and in decay; with the process of oxidation in living tissues; and with the synthesis and decomposition of many organic substances. Indeed, most of the metabolic processes of plants and animals are probably dependent, in one way or another, upon enzymes.

It is only the digestive enzymes and their activities which are to be considered here. Digestion is generally accompanied by *hydrolysis*, or the addition of one or more molecules of water to a molecule of the substance to be digested. The sugars are soluble and most of them may be assimilated directly without digestion. Cane sugar, however, is often broken down into glucose and fructose through the agency of the enzyme *invertase*, thus:

$$\underset{\text{Cane sugar}}{C_{12}H_{22}O_{11}} + \underset{\text{Water}}{H_2O} = \underset{\text{Glucose}}{2C_6H_{12}O_6}$$

Maltose is also converted into glucose by *maltase*. Far more important than these changes, however, is the digestion of

starch through the action of *diastase* and other enzymes, with the ultimate production of glucose, thus:

$$\underset{\text{Starch}}{C_6H_{10}O_5} + \underset{\text{Water}}{H_2O} = \underset{\text{Glucose}}{C_6H_{12}O_6}$$

The reserve celluloses are broken down by hydrolysis into various sugars through the action of another enzyme, *cellulase*. Fats, by the agency of *lipase* and similar enzymes, are broken into glycerine and fatty acids, which may be absorbed into protoplasm. Protein-digesting enzymes are necessarily numerous, but two of them, *pepsin* and *trypsin*, are especially important. The former converts proteins into water-soluble peptones and proteoses; the latter carries the process still further with the ultimate production of amino acids. It should be noted that all these types of digestion are carried on within the protoplasm of living cells throughout the plant body wherever digestion is necessary, and not in the cavities of special digestive organs.

Assimilation.—After a food has been digested, it must then enter the protoplasm of a cell and become an integral part of the living substance. This process is known as *assimilation*, and is the central problem of metabolism. From the activities of protoplasm it is clear that this remarkable material must be very complex, both chemically and physically. It is highly unstable and is continually undergoing processes of construction and destruction. Although one can trace with some confidence the entrance into protoplasm of certain comparatively simple substances and the departure therefrom of others equally simple, little is known as to the happenings which take place between these two events. It is here that dead matter becomes alive, and that inert food substances become endowed with the unique properties of living protoplasm. This change never occurs spontaneously in nature, but is always brought about through the activity of protoplasm already existing, all the evidence at hand indicating that life always comes from life and in no other way. Although this process is going on continually in every living plant and animal, man has as yet been unable to master its intricacies or to bring it to pass in the laboratory.

Respiration.—Those physiological changes which involve the progressive elaboration of organic substance reach their climax in the production of protoplasm. This constant upbuilding

and renewal of the living material is succeeded by an equally constant process of disintegration, which results in the liberation of energy and which usually is accompanied by the intake of oxygen and the outgo of carbon dioxide. This general process is termed *respiration*.

Before entering upon a detailed study of this important phase of plant physiology, one should understand clearly the phenomena involved in the energy relations of the plant, to which not only the process of respiration but also those of food synthesis and nutrition essentially belong. Like every living thing, the plant is continually active. This activity shows itself in movement of various sorts, either of the plant body as a whole, of the substances within it, of atoms and molecules during those chemical changes which are always taking place in living cells, or of plant tissues in the phenomena of growth. These various movements, the maintenance of which is necessary if the plant is to remain alive, require the expenditure of *energy*, as do all movements of matter; and one of the chief problems in the economy of the plant, as in the operation of any machine, is to obtain an adequate supply of energy and to liberate it at the proper times and in the proper places.

Kinetic and Potential Energy.—Energy exists in the universe in two forms: active, or *kinetic*, and stored, or *potential* energy. Kinetic energy performs work by setting matter in motion, either by changing its position, by raising its temperature, by producing chemical alterations within it, or in other ways. Potential energy is inactive energy, stored up in an object by virtue of the position or condition of that object. Potential energy exists in a stretched spring, in a bent bow, in the water of a mountain stream, in a charged battery, in a piece of coal, or in an explosive. It is present in an object *only as the result of the previous expenditure of kinetic energy upon that object.* Care should of course be taken not to confuse this "storage" of energy with the storage of food or any other form of *matter.* The presence or absence of a supply of stored energy in a given body merely affects the relations between its parts and does not alter in the least the bulk of the object or the amount of matter which it contains. One needs only to remember that a bent spring weighs no more than an unbent one or a charged battery than an uncharged one. *Energy* and *matter*, at least in ordinary experience, are fundamentally distinct.

Release of Stored Energy.—The potential energy in an object may at any time, under an appropriate stimulus, become converted again into kinetic form and do work, as when the stretched spring moves the mechanism of a watch, the bow moves an arrow, the falling water moves a mill wheel, the battery moves a telegraph sounder, the burning coal converts water into steam which moves a machine, or the explosive moves a projectile. In all of these cases the supply of stored energy is finally exhausted and motion ceases. In this process of converting potential into kinetic energy or the reverse, no energy is gained or lost, the total amount remaining constant.

A machine is anything which controls and directs the liberation of energy so that work of a particular kind is done at a particular place and time. One of its prime necessities is an ample supply of potential energy, and in the machines which are most familiar this is available in the form of wood, coal, oil, or stored electricity. The living organism resembles a machine in the fact that it, too, directs the expenditure of energy, and it therefore needs a plentiful supply of this energy in potential form which it may liberate, in the process of respiration, at any point throughout its body for the performance of its many activities. The fuel which the organic machine uses in this process is known as *food*, and the potential energy within this food came originally from the kinetic energy of sunlight and was converted into potential form by photosynthesis in the green cells of the leaf. Food resembles wood, coal, or oil in being a somewhat unstable chemical compound which, through the addition of oxygen, will break down rapidly and resolve itself into simpler components, usually carbon dioxide and water, and by this means release the potential energy it contains. This process of oxidation is common in nature. In ordinary fuels it takes place only at high temperatures and is then known as combustion. In living organisms it can go on at much lower temperatures and here is known as physiological combustion or respiration. In their essential feature—the liberation of energy in kinetic form by the breaking down of complex and unstable chemical compounds into simpler ones through the addition of oxygen—respiration and combustion are essentially similar.

A machine is supplied with fuel (its "food") by an operator, and an animal obtains its food by seizure, but the food which a green plant consumes must be secured through the plant's own

activities. The significance of the food-making process called photosynthesis is now more evident than before. The kinetic energy which the plant, through its chlorophyll, absorbs directly from the light of the sun is here used to do the work of breaking up carbon dioxide and water and reuniting these atoms into the simple food glucose. The energy expended in accomplishing this union is obviously stored up in potential form in the molecules of glucose and of the other foods or plant materials which may be derived therefrom, just as the energy expended in winding a clock is stored up in the compressed mainspring. Under appropriate conditions this potential energy may be liberated anywhere and at any time to do work in any organism. One of the most important principles of physiology is thus made evident—that food is merely the medium by which energy received from the sun intermittently and only in certain exposed organs is stored up, carried to all parts of the plant (or animal), and made available for work at all times and in all places. This conception has been formulated concisely in the metaphor that "food is a 'storage battery,' charged in green leaves by the sun and discharged in the body by respiration."

The Importance of Photosynthesis.—The importance of photosynthesis to the organic world lies in the fact that this process is practically the only means whereby living things can store up energy. Green plants, the ultimate providers of all foods, are the sole agencies through which the animals and man can tap the abundant supplies of energy in the universe and obtain therefrom a sufficient quantity to maintain their varied activities. This energy is all stored originally in the molecule of glucose, and before it is converted again into kinetic form may pass through scores of modifications and enter into the composition of the bodies of a dozen successive organisms. Although kinetic energy is streaming upon the earth daily in enormous quantities from the sun, only the chlorophyll-bearing plants are able to use it directly. Even in industry man still depends very largely upon photosynthesis, since the energy which he releases from wood, coal, and oil was originally locked up in these substances, in some cases millions of years ago, by the photosynthetic activity of green plants.

Respiration and Life.—With an understanding of the significance of the plant's energy relationships and the part which respiration plays therein, a more detailed study of respiration

itself may be undertaken. This process, unlike photosynthesis, is not carried on in particular organs and under particular conditions, but is universal, taking place under all conditions and in *every living cell.* Respiration, indeed, is believed to be a necessary accompaniment of life itself, as might be inferred from the fact that living protoplasm is continually active and is thus continually expending energy. Even in cells which show no other external signs of life, respiration, though very feeble, may still be detected. The amount of respiration which takes place is a rough index of the activity of the cell, organ, or organism studied, being relatively high in growing tissues and relatively low in dormant ones.

The liberation of energy is the essential feature of respiration and the addition of oxygen is its usual accompaniment, particularly in the higher plants; but in certain cases and under certain conditions, notably among some of the lowest members of the plant kingdom, respiration may be carried on in the absence of oxygen. These two types are recognized as *aerobic* and *anaerobic* respiration. They are so different as to require separate consideration.

Aerobic Respiration.—Aerobic respiration is essentially an oxidation process. Free oxygen is added to organic substances (chiefly carbohydrates) with the consequent breaking down of the latter into their original inorganic components, carbon dioxide and water, thus:

Glucose		Oxygen		Carbon dioxide		Water
$C_6H_{12}O_6$	+	$6O_2$	=	$6CO_2$	+	$6H_2O$

The oxygen usually is taken directly from the atmosphere through stomata, lenticels, or other openings.

This process of oxidation is one of those chemical changes which are assisted by enzymes, and the oxidizing enzymes or *oxidases* occur in every living cell. As to whether it is the protoplasm itself or unassimilated food substance within the protoplasm which is oxidized, there is some difference of opinion. It is certain, however, that most of the carbohydrates and fats which are taken into the protoplasm soon furnish, either directly or indirectly, the material which is oxidized in respiration. Proteins, although their chief function is constructive, undoubtedly

also contribute to the supply of oxidizable substances. Whatever nitrogenous waste material is given off in their disintegration, however, must immediately be assimilated again, for (at least among the higher plants) nitrogenous compounds do not appear among the products of respiration.

Carbon dioxide is almost invariably a product both of aerobic and of anaerobic respiration. Indeed, the evolution of this gas, even in minute amounts, is regarded as proof that the organism is respiring and therefore alive. The amount of oxygen taken in and the amount of carbon dioxide given off are in the long run equal, though under certain conditions one may temporarily exceed the other.

Most of the energy liberated in respiration eventually manifests itself as heat, and a respiring organism will therefore tend to raise the temperature of its surroundings. This heat ultimately will become dissipated into space and lost forever to organisms. If it were not for the energy of light continually reaching the earth from the sun, the supply of energy available for the activity of living things would therefore soon become exhausted.

By comparing the chemical equations for photosynthesis and aerobic respiration, it will be seen that one is the precise reverse or reciprocal of the other. Photosynthesis adds carbon dioxide to water and produces sugar and oxygen. Respiration adds oxygen to sugar and produces carbon dioxide and water. These two processes actually may be going on in the same tissue at the same time, a circumstance which has made the study of plant metabolism peculiarly difficult, since one activity may mask the other. Photosynthesis, however, is confined to the chlorophyll-bearing cells and occurs in them only in the presence of light. In such cells there is a preponderance of photosynthesis in the daytime and of respiration at night. For a brief period in the morning and again in the evening, and for longer times when illumination is low or other conditions unfavorable for photosynthesis, the two processes may balance each other exactly, the tissues giving off in photosynthesis just the amount of oxygen which is necessary to carry on their respiratory activity. Respiration, unlike photosynthesis, occurs in every living cell.

Comparison between Photosynthesis and Aerobic Respiration.—A brief comparison between photosynthesis and respiration is presented in tabular form below:

Photosynthesis	Respiration
Stores energy	Releases energy
Absorbs carbon dioxide	Liberates carbon dioxide
Liberates oxygen	Absorbs oxygen
Takes place only in green plants	Takes place in all plants and animals
Takes place only in chlorophyll-bearing cells	Takes place in all living cells
Constructs food	Destroys food
Increases weight	Decreases weight

In its essential characteristics—intake of oxygen, liberation of energy, and raising of temperature—the aerobic respiration of plants is exactly comparable to the respiration of animals, a fact which the complexities of plant metabolism sometimes obscure.

Anaerobic Respiration (Fermentation).—Anaerobic respiration, in which the breaking down of chemical compounds and the consequent liberation of energy is not accompanied by an intake of free oxygen, is characteristic of certain lower plants and sometimes of higher ones when temporarily deprived of oxygen. The best known examples of this process are alcoholic fermentations and allied phenomena. These were named "fermentations" from the fact that the activity of ferments (now more commonly called enzymes) was here first clearly shown. There is consequently a confusion in the application of the term *fermentation*, the commonest usage regarding it as practically synonymous with anaerobic respiration, the other expanding it to cover all activity brought about by the agency of enzymes.

The most important characteristic of anaerobic respiration is the fact that it does not lead to a complete breaking down of the organic substance or food but only to its partial decomposition, with the result that a quantity of more or less complex by-products are necessarily formed which still contain a considerable amount of potential energy. The accumulation of these by-products often stops the process itself.

The fermentation of sugar by yeast is the classic example of anaerobic respiration. The yeast plants—minute, single-celled organisms—thrive in rather weak solutions of sugar. Those which have easy access to the air usually respire aerobically, but if the supply of free oxygen is limited (as is the case anywhere below the surface of the liquid) or if it becomes exhausted, the yeast respires anaerobically. The cells now obtain their energy

through a *partial* decomposition of the sugar, with the formation of carbon dioxide and a complex by-product, ethyl alcohol, thus:

$$\underset{\text{Glucose}}{C_6H_{12}O_6} = \underset{\substack{\text{Carbon}\\\text{dioxide}}}{2CO_2} + \underset{\text{Alcohol}}{2C_2H_5OH}$$

It is evident that only a portion of the potential energy in the sugar has been liberated, for the resulting alcohol may be absorbed by another organism, or may be burned, and will then yield a considerable amount of additional energy. When the concentration of alcohol has reached a certain point, it poisons the yeast plant and fermentation ceases.

The respiration of other minute plants may also bring about alcoholic fermentation, and still others produce fermentations of different types, such as those having for their by-products butyric acid (in the spoiling of butter), lactic acid (in the souring of milk), and various others, many of which are of economic importance. In all these cases energy is liberated and may be detected by the consequent rise in temperature, which is often more marked than in aerobic respiration.

Certain micro-organisms are exclusively anaerobic and are actually killed by the presence of free oxygen. Others, like yeast, may respire either aerobically or anaerobically, depending upon the external conditions.

The decay of dead organic matter is due almost entirely to the respiration of micro-organisms. If the material is exposed freely to the air, bacteria will break it down rapidly and completely by their aerobic respiration. If free oxygen is unavailable, as is the case within a large mass of dead organic material, the process is carried on anaerobically and is slower and more complicated. Here a whole series of micro-organisms, each specific in its activity, are successively concerned. One type will break down the organic substance partially, extracting a certain amount of the potential energy which it contains. In its altered chemical state and with its diminished supply of energy, the remaining material is now seized upon by another type of micro-organism and, entering into the anaerobic respiration of this form, is broken down still further and loses still more of its potential energy. This process continues until finally the whole of the material (except its mineral constituents) passes into the

atmosphere as carbon dioxide, water, and nitrogen, the original materials out of which organic substance is constructed.

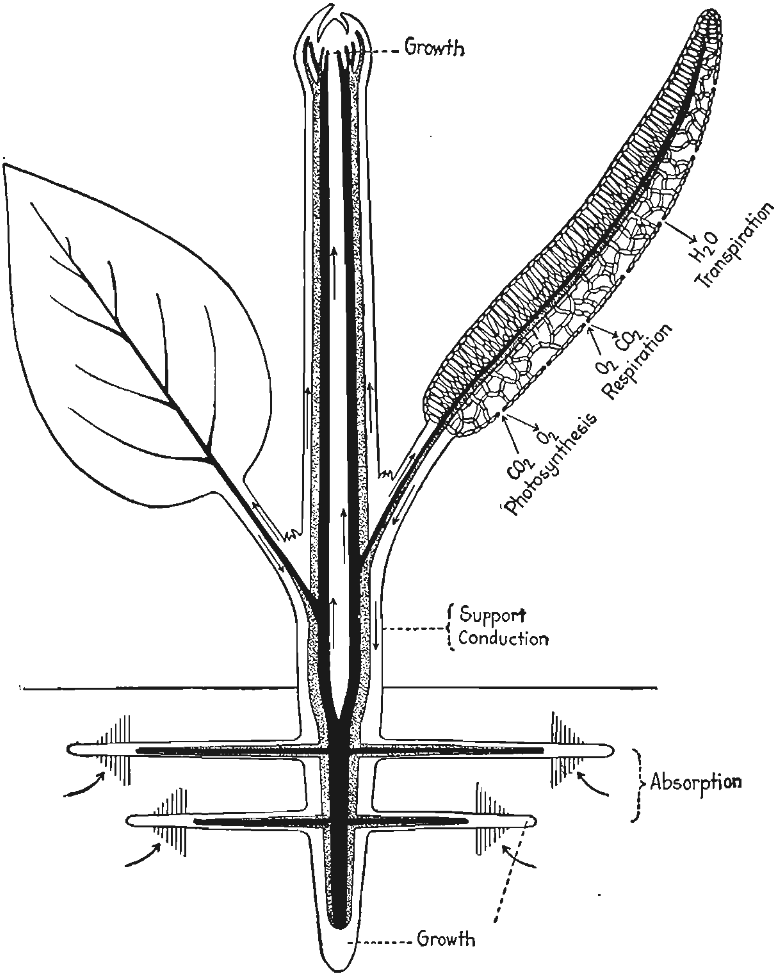


FIG. 76.—Important structures and functions of the plant. Diagrammatic representation of roots, stem, leaves, and growing regions and their functions. Wood solid black, phloem dotted, pith and cortex white. Arrows indicate movement of materials into the plant, along the stem, and to and from the leaves. One leaf is represented in section. Water passes from the root upward to stem and leaves through the wood. Manufactured food passes from the leaves both upward and downward through the phloem. The various gas exchanges between leaf and atmosphere are graphically represented.

The structure and activities of the root, the stem, and the leaf have now been considered, and the functions of absorption,

conduction, photosynthesis, respiration, and transpiration discussed. These are the main vegetative structures and functions of the plant body, and are set forth graphically in Fig. 76.

QUESTIONS FOR THOUGHT AND DISCUSSION

321. Which of the three main types of food makes up the largest part of the diet of animals and man?

322. What advantage is it to the plant to have its carbohydrate food stored chiefly in the form of starch rather than as sugar?

323. What is it that makes fats very concentrated foods?

324. Why are proteins "far more effective than any other foods in the construction and renewal of living substance?"

325. Why do plants belonging to the Legume family usually contain more protein than most plants?

326. Where and when in a plant would you expect digestion to take place most vigorously?

327. What important difference is there between the process of digestion in plants and the process as it most commonly occurs in animals?

328. Just how does the food which is stored in the endosperm of a seed (see page 232), and which is therefore not in the embryo itself, become available to the young plant?

329. In what way do the insects captured by an insectivorous plant become available to it as food?

330. Why do parsnips taste so much sweeter in early spring than they did in the previous fall?

331. Why are vegetables like peas and sweet corn much sweeter in their young and immature state than when they grow older?

332. Maple sap is very sweet in the spring but contains almost no sugar in the summer. Explain.

333. Hay harvested before its seed is ripe has much more feed value than it has a few weeks later. Explain.

334. Certain fungi attack wood, their very delicate, thread-like branches penetrating into the hard, woody tissues and destroying them. How is it possible for them to do this?

335. Give three examples from every-day life (aside from those mentioned in the text) of the conversion of kinetic into potential energy and its subsequent release again in kinetic form.

336. What is the ultimate source of all energy liberated in the bodies of plants and animals? Explain.

337. Just where in the plant body is kinetic energy changed into potential energy, and just where is potential energy changed into kinetic?

338. What was the original source of the heat liberated in the burning of wood? of the energy used in driving an automobile?

339. What important sources of energy used by man in his industries owe their origin to photosynthesis? Which ones do not?

340. Is the sum total of photosynthetic activity or of respiratory activity the greater in a normal green plant? How do you know this?

341. Why is an excretory system, so common in animals, absent in plants?

342. How is it possible for oxygen to enter a living cell from the air?

343. How is oxygen able to reach cells situated far within the plant body and thus away from the outside air?

344. From your knowledge of plant morphology, what structures do you think are chiefly concerned in the entrance of oxygen from the air into (1) a young, growing root; (2) a leaf; (3) a woody twig; and (4) an old trunk?

345. How do submersed water plants obtain oxygen?

346. Plants which live in bogs or very wet places usually have large air chambers in their tissues, particularly in roots or other subterranean parts. Explain.

347. Do you think that growing plants are good things to have in a sick room? Explain your answer.

348. If a plant were to be grown in air which had been freed of oxygen, would it live longer in darkness or in light? Explain.

349. A seedling plant which has sprouted and grown in a dark place will have a dry weight which is actually less than that of the seed from which it grew, although the bulk of the seedling is far greater than that of the seed. Explain.

350. Why is it physiologically impossible for a seed to maintain its vitality and germinating power indefinitely?

351. Does the increase in dry weight of a plant accurately represent the amount of photosynthesis which has taken place in it? Explain.

352. Which of three identical wooden posts will remain sound longest: one left freely exposed to the air; one driven into the soil (as a fence post); or one driven under water (as a pile)? Explain.

353. Most of the fossils of animals and plants which have come down to us were preserved in swamps rather than on high ground. Explain.

354. Why is it necessary to change the water in an aquarium frequently if animals are living in it alone, but infrequently, if at all, when green water plants are living in it alone?

355. Where in a plant would you expect to find the highest temperature?

356. The internal temperature of plants is not far from that of their surroundings; in the higher animals it is usually much above that of their surroundings. Explain this difference.

357. Why do land animals need to have lungs for inhaling and exhaling air, whereas such structures are unnecessary in plants?

358. Which will weigh more, a piece of sound wood or the same piece after wood-decaying fungi have been growing in it for a time? Which will yield more heat when burned? Explain.

359. Why do plants in glazed pots grow poorly?

360. Why should pebbles, bits of broken pottery, or similar coarse materials be placed in the bottom of a flower pot in which a plant is to be grown?

361. In propagating a plant by "cuttings," a small shoot is cut off and the cut end placed in damp soil, where it takes root. Sand is much better than a heavy, clayey soil for rooting cuttings in this way. Explain.

362. Why will all cut flowers keep longer in a refrigerator than at ordinary room temperatures?

363. In cranberry bogs which have been flooded for a few days in the fall to protect them from frost, the unripe berries suffer much more from "smothering," due to lack of oxygen caused by the flooding, than do the mature, fully ripe ones. Explain.

364. Fermentation often generates a considerable gas pressure, but aerobic respiration does not. Explain this difference.

365. What happens when bread dough is "raised" with yeast?

366. Why is it important to boil down maple sap as soon as it is drawn from the tree?

367. When jars of preserved fruit "spoil," why do the covers sometimes blow off?

368. A foundation of manure under a "hot-bed" will keep the soil warm. Explain.

369. Give at least two reasons for lifting the glass from a hot-bed in the middle of a sunny day.

370. If hay which has not been thoroughly dried is stored in a barn, it introduces a danger of fire there. Explain.

371. The danger mentioned in the previous question is much less if the damp hay is sprinkled liberally with salt, and if the barn is very tightly built. Explain these facts.

NOTE.—A silo is a large, tank-like structure, open at the top. Green and living corn plants, chopped up into small pieces, are packed tightly into the silo in the fall and fed to cattle during the winter.

372. What prevents the contents of a silo from decaying?

373. During the first few days after a silo is filled, its contents becomes distinctly warm, and it then gradually cools off. Explain.

374. Why is it necessary to have the walls of a silo built very tightly?

375. If the contents of a silo is not packed down tightly, it is likely to spoil. Explain.

376. Why does the surface layer at the top of the silo often spoil?

REFERENCE PROBLEMS

81. Give an example of a plant which is particularly rich in starch; in fat; in protein.

82. What is the relative production of energy per unit of weight by a carbohydrate, a fat, and a protein?

83. Do fats play a more important part in animal or in plant nutrition? Explain.

84. In general, how may "organic" substances be distinguished from "inorganic" ones? Why were these terms chosen?

85. What are vitamines? Where are they produced in plants? What is their importance in animal nutrition?

86. In what ways may the dormancy of plant parts, such as bulbs, buds, and seeds, be broken so that growth may begin at once?

87. What is known as to the precise role in plant nutrition of each of the "essential" chemical elements?

88. What has been the history of a piece of coal and why does it produce so much energy when burned?

89. What are cypress "knees" and what is their function?

90. What non-gaseous and unusable waste products sometimes result from plant metabolism, and what becomes of them?

91. What plants derive energy from the oxidation of other compounds than those of carbon?

92. Give the author and title of three important books dealing with some phase of plant metabolism (aside from photosynthesis), and outline briefly the content of each.

93. Name several botanical investigators who have done important work in respiration or some other field of plant metabolism and state the notable contributions made by each.

94. Give the derivation of the following terms and explain in what way each is appropriate:

Metabolism	Enzyme	Respiration
Digestion	Assimilation	Fermentation

CHAPTER VIII

GROWTH

A large part of the food which a plant manufactures is used as a source of energy, and as the potential energy it contains is liberated in kinetic form through the process of respiration, the food breaks down again into those simple components out of which it was constructed. Food may be thus consumed soon after it is produced, or it may be stored and used as a source of energy for the plant or its offspring weeks, months, or even years later. A healthy plant, however, manufactures more food than is necessary to maintain the activities of its living substance, and the surplus may be built, more or less permanently, into its tissues, producing new protoplasm and new cell walls and thus promoting the *growth* of the plant body. Growth represents the excess of constructive over destructive metabolism. A knowledge of what it involves and of how it takes place is evidently necessary if one is to arrive at a clear understanding of the structure and the development of plants.

The term "growth," in its simplest usage, refers to any *increase in size*, either of the whole organism or of its parts. This expansion may be a mere swelling brought about by a vigorous absorption of water, or it may be due to an increase in bulk of actual plant material—protoplasm and the dead structures secreted by it. All early stages in growth are of the former type, and the swollen and succulent tissues thus produced gradually attain to normal firmness through the deposition within them of large amounts of new material. Indeed, early growth may be accompanied by an actual, though temporary, decrease in dry weight.

In studying this process of growth in the plant as a whole it should be remembered that the plant body is made up of a mass of minute cells. The size of the cells in any particular tissue and within the same species is rather constant, and is believed to approximate the most efficient size for that particular tissue. Very large cells and very small cells evidently would possess many disadvantages. It is therefore clear that growth must

consist in the production of more cells rather than in the enlargement of those already present; and the method by which new cells are formed and added to the plant body deserves careful study in a consideration of the growth process.

The Formation of New Cells.—In the previous discussion of the plant cell (Chapter III), this was shown to consist of a small mass of protoplasm in which two portions may be distinguished; the relatively undifferentiated ground mass or *cytoplasm*, and a denser and more or less spherical body within this, the *nucleus*. About the whole is a cellulose wall deposited by the protoplasm. In growing tissues where cell multiplication is proceeding, this wall is very thin, and the single vacuole, so conspicuous in mature cells, is ordinarily represented by a large number of much smaller ones. In the formation of new cells at such growing regions, and the development therefrom of new tissues, three stages may be distinguished: *cell division*, in which the number of cells is increased by the repeated division of certain of them into two; *cell enlargement*, in which these new cells expand rapidly to their final size; and *cell maturation*, in which they assume their mature structure and characteristics.

Cell Division.—Cell division is not the simple splitting of a cell into two parts, but is accomplished in a rather complex fashion. Dividing cells are ordinarily much smaller than those of the mature tissues to which they give rise, and are very uniform in structure. The nucleus, here relatively large in proportion to the rest of the cell, is the structure which takes the most active part in division, for before the entire cell divides into two the nucleus itself does so by a characteristic process known as *mitosis* (Figs. 77 and 78). This cannot well be studied in living tissue, and a knowledge of it has been derived from microscopic examination of thin sections which have been carefully prepared and stained.

Within the nucleus of any cell which is not undergoing division and which in respect to this process is said to be in a "resting" condition, there is a network, often very fine and hard to distinguish as such, consisting chiefly of a substance which stains very deeply with certain dyes used in the study of cell structures and which hence has received the name of *chromatin*. When a cell is preparing to divide, the first visible change is a condensation of this nuclear net into a stouter thread or *spireme*, which is much twisted but seems in most instances to be a single continu-

ous structure. This stage in nuclear division is known technically as the *prophase*. The spireme thread soon divides into a number of units, often in the shape of irregularly curved rods, the *chromosomes*. For any given species the number of chromo-

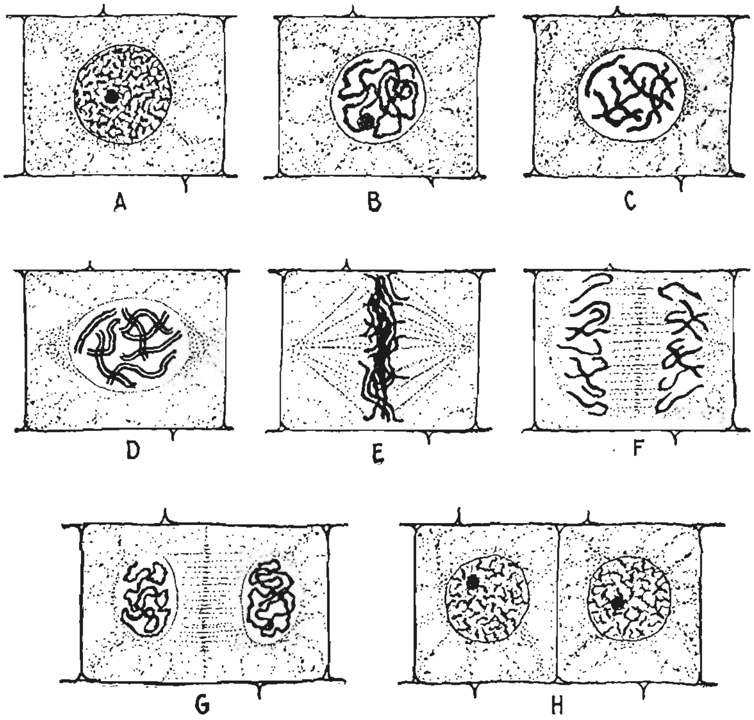


FIG. 77.—Cell division by mitosis. *A*, resting cell, the chromatin of the nucleus in a fine network. *B*, the chromatin is gathered into a long thread. *C*, this thread breaks up into chromosomes. *D*, each chromosome splits into two lengthwise. (*B*, *C*, and *D* are called *prophases*.) *E*, *metaphase*. The split chromosomes arrange themselves in a plane across the equator of the cell, and the spindle, with its two poles, is formed. *F*, *anaphase*. The chromosome halves separate, one complete set (eight in this case) going to one pole and the other set to the other pole. *G*, *telophase*. Each new group of chromosomes arranges itself into a thread and a new cell wall begins to appear between the groups. *H*, two complete new cells, each with a nuclear content equal and similar to that of *A*.

somes in the cell is characteristic and constant. Thus in the body cells of the lily there are always 24, in those of the onion 16, and in those of the pea 14. Furthermore, each chromosome is not merely an undifferentiated mass of chromatin but has its own individual size and shape which is repeated at every cell

division and which can often be recognized by the skilled observer. Each chromosome now splits exactly into two, its halves still lying side by side. At about this time two *poles* or apparent centers of attraction arise in the cytoplasm on opposite sides of the nucleus, and from each of these poles a mass of delicate fibers radiates inward to the nucleus. The nuclear membrane now disappears and the fibers extend into the nucleus, some of them becoming attached to the chromosomes and others extending continuously from one pole to the other, the entire fiber system being known as the *spindle*. The chromosome pairs now

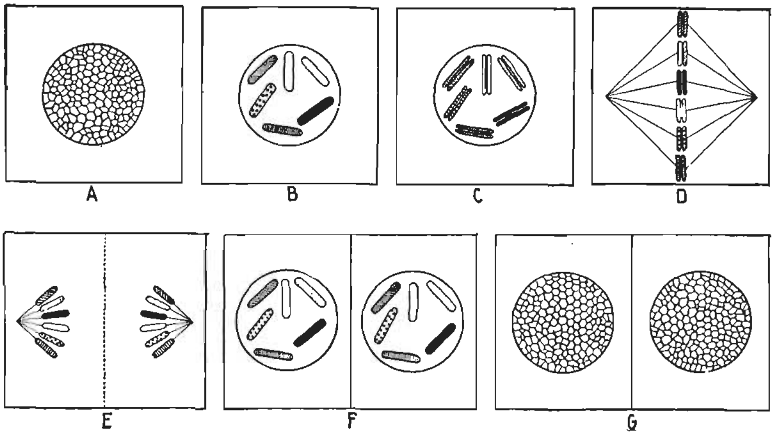


FIG. 78.—Diagram of mitosis in an ordinary body-cell. *A*, resting nucleus; *B* and *C*, prophases; *D*, metaphase; *E*, anaphase; *F*, telophase; *G*, new cells. The separate chromosomes, each of which has an individuality of its own, are differently marked. It is evident that the chromatic material is divided exactly evenly between the two daughter cells. (*Modified from Sharp.*)

move into a plane or *equatorial plate* stretching across the cell at right angles to the spindle, the attainment of this stage marking the *metaphase* of division. Each chromosome has a spindle fiber attached to it, sometimes at the end, sometimes near the middle; but for the two members of a pair (the two halves of each of the original chromosomes) the fibers run to opposite poles. The contraction of the spindle fibers which now takes place therefore pulls these halves apart, one group of chromosomes moving toward one pole and an entirely similar group moving toward the other, a stage designated as the *anaphase*. Each chromosome group now becomes aggregated into a tangled mass from which a new chromatin net develops and around which a

nuclear membrane makes it appearance. Meanwhile a new cell wall is being laid down between these two nuclei, usually through the appearance of minute thickenings at the middle points of the fibers which still connect the nuclei, and the union of these thickenings into a continuous *cell plate* which ultimately extends entirely across the cell. This stage, the *telophase*, is followed by the splitting of the cell plate into two layers and the deposition between them of a new cell wall, which completes the division of the mother cell into two similar daughter cells. This complicated process is apparently concerned with the accomplishment of an exactly equal division of the chromatin material between the two daughter cells and thus among all the cells of the plant body, suggesting the conclusion, which receives support from a large body of other evidence, that the chromatin is of the utmost importance in directing the growth and differentiation of the organism.

Cell Enlargement.—Although two new cells have now been formed, these still occupy together a space no larger, ordinarily, than the size of the cell from which they arose, so that no real growth as yet has taken place. The abundance of sugar and other dissolved materials, however, which are continually flowing toward such a growing region, causes water to be drawn into them vigorously by osmosis. Since the walls are still thin and elastic, they stretch readily and the small cells thus soon increase to the size of the mother cell. They may now proceed to divide again just as before; but if they are situated near the edge of the zone of cell division, one or both of them may instead continue to increase markedly in size until the final and permanent volume is attained. During this rapid expansion, the size of the nucleus and the amount of cytoplasm increases little if at all, but the droplets of clear liquid, or *vacuoles*, which occur within the cell enlarge and coalesce until, in most tissues, they merge into the single *sap cavity* which occupies the whole central region and which is so characteristic of mature plant cells in general. The cytoplasm is now a thin sac surrounding this sap cavity and pressed closely to the wall; and the nucleus has also been pushed out of the center of the cell and, often somewhat flattened, lies against the wall at one side. This process of cell enlargement by absorption of water, following the increase in number of cells by division, causes most of the obvious increase evident in the size of plant parts. It also is probable that, at least in certain

cases, a portion of this increase is due to the swelling of colloidal materials, in cell wall and protoplasm, as water is absorbed.

Cell Maturation.—The new tissue thus formed is soft and weak, owing to the thin walls of its component cells, and the third stage in growth, cell maturation, is brought about by the transfer of an abundant supply of food into these newly formed parts and the consequent construction therefrom of additional materials, chiefly in the cell wall, until the cells have reached the normal mature condition characteristic of the particular tissue of which they form a part.

Growing Points and Their Function.—Such, in brief, is the history of the production of new cells by which the growth of the plant body takes place. It is evident, however, that in mature plant tissues, where the cells are surrounded by thick, firm, and dead walls, cell division is difficult or impossible. Such tissues are really locked within their own walls and can grow no further. Organs like the leaf and flower, which rapidly attain a rather definite size beyond which growth no longer takes place, do not present this problem; for here the organ develops from a small mass of growing tissue, enlarges rapidly throughout its whole extent, and reaches maturity in all its parts essentially at once, when growth stops. In such organs as the root and stem, however, where growth continues more or less indefinitely and where the great bulk of the tissues are necessarily mature and functioning, there obviously must be some way of insuring the continued production of new cells. This is accomplished through the activity of *growing points* or *meristems*, which are merely groups of cells remaining in an embryonic and undifferentiated condition, thin walled and packed with protoplasm. These groups of permanently "young" cells occupy regions where growth is to take place, as at the tip of the root or stem or at the cambium. Such a growing point may long remain dormant; but when it becomes active, cell division begins again within it. The newly formed cells which lie next to the already mature tissue now undergo enlargement and become themselves mature. This process does not affect all of the cells of the growing point, however, for the portion away from the maturing cells still remains undifferentiated and continues to serve as a center of production for young cells which are to be added to the tissue. The growing point is thus a rather small and inconspicuous group of cells, not increasing in bulk itself, but carried progressively

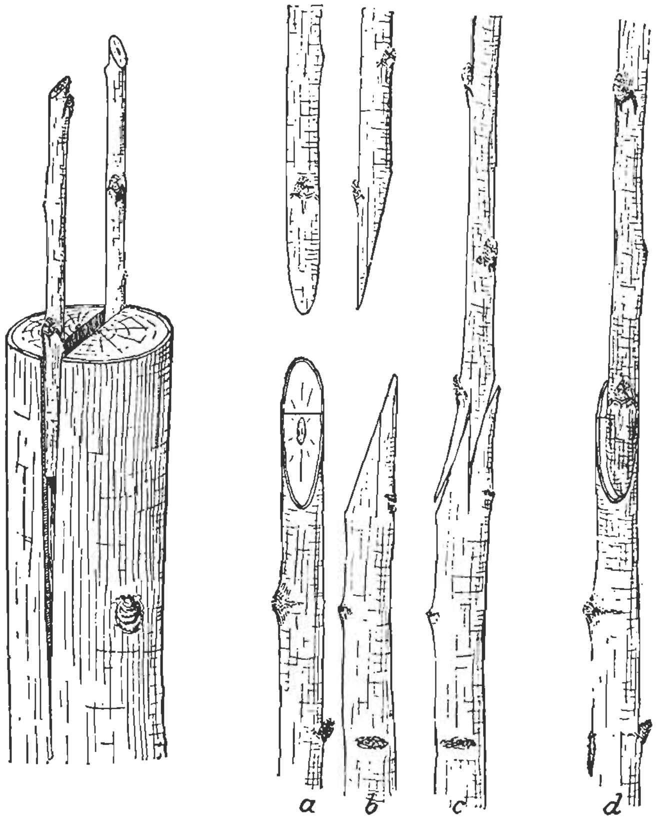


FIG. 79.—At left a cleft-graft, showing method of inserting scions into stock. At right, a whip or tongue graft. *a* and *b*, front and side views of scion (below) and stock (above) showing method of cutting. *c* and *d*, insertion of scion into stock. (*From Gardner, Bradford, and Hooker.*)

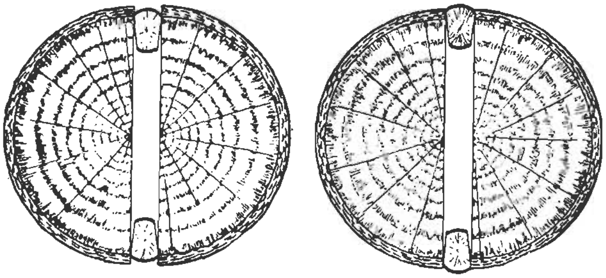


FIG. 80.—Diagram of a transverse section across a cleft-graft. At left, scions inserted correctly, the cambium of stock and of scion in contact. At right, incorrect insertion, the cambial layers not in contact. (*From Cardinell and Bradford.*)

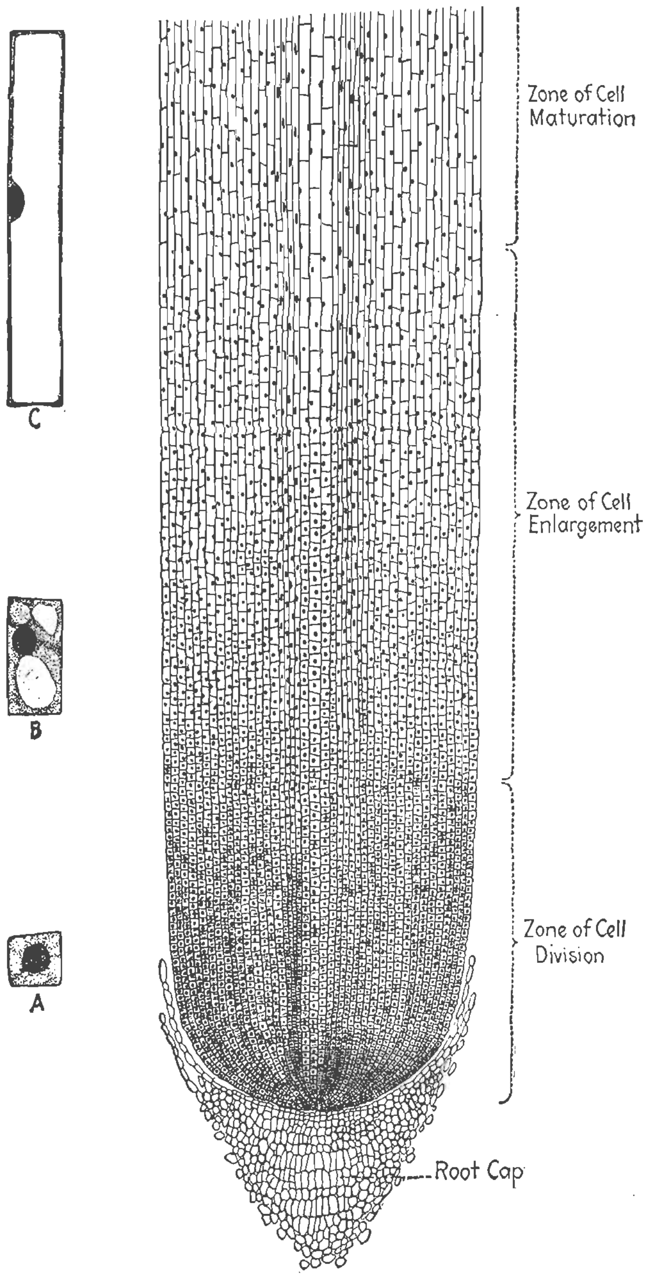


FIG. 81.—Longitudinal section of a growing root. In the zone of cell division the cells are small, rich in cytoplasm and rapidly dividing by mitosis. In the

outward on the crest of the tissue which it creates. It may perhaps be compared with a layer of coral animals, which by their activity build a reef farther and farther outward and are carried out upon it; or to a brick layer constantly adding bricks to the top of a wall and being carried up himself by the wall which he has made.

This method of growth at a definite point or layer through the activity of a meristem, which is so characteristic of plant tissues and so different from that employed in the growth of animals, has certain consequences worthy of mention. It writes in the body an almost complete history of the plant's growth and development, for many of the first-formed tissues are still present (unless lost through decay), buried in the successively later accretions which have been steadily added. A careful internal and external examination of a tree trunk, for example, would enable one to tell almost exactly how tall and how thick the tree was at any year in its past history. An understanding of the location and activity of growing points is essential in the practice of the various methods of grafting and budding, for these are necessarily concerned with a manipulation of the meristematic regions (Figs. 79 and 80).

There are many more actual or potential growing points in the plant body than ordinarily develop, but under appropriate conditions any of them may begin to grow. Furthermore, certain cells in mature tissues may occasionally become rejuvenated and begin to divide again, as is well shown in the healing of those wounds which occur in regions lacking meristematic tissue.

There are two general types of growing points in most plants—*terminal* and *lateral.* The former, which develop at the tips of roots and stems, cause an increase in the *length* of these organs, and through their activity the stem grows tall and its roots spread farther into the soil. The latter, of which the *cambium* is the characteristic example, forms a ring or sheath of growing tissue encircling the root and stem throughout their entire extent and causing these organs to increase in *thickness.*

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zone of enlargement, the cells are no longer dividing but are rapidly elongating. Vacuoles or sap cavities are beginning to increase in size in the cytoplasm. In the zone of maturation the cells have attained their final size, and the center of each is now occupied by a large sap cavity, surrounded by a thin layer of cytoplasm. In this zone (only a part of which is shown) the cells are beginning to assume their mature characteristics, and differentiation of the tissues in taking place. *A*, *B*, and *C*: cells from these three zones, much enlarged.

Terminal Growing Points.—The growing tip of a root furnishes a good example of a terminal growing point, and a brief study of this region perhaps will provide a clearer understanding of how such a tissue functions (Fig. 81). At the very tip of the root is the root cap, a body of dead cells continually renewed from the growing point within as they are sloughed off by friction, and which protects the delicate root tip as it is forced through the soil. Just back of this is the zone of cell division, a relatively

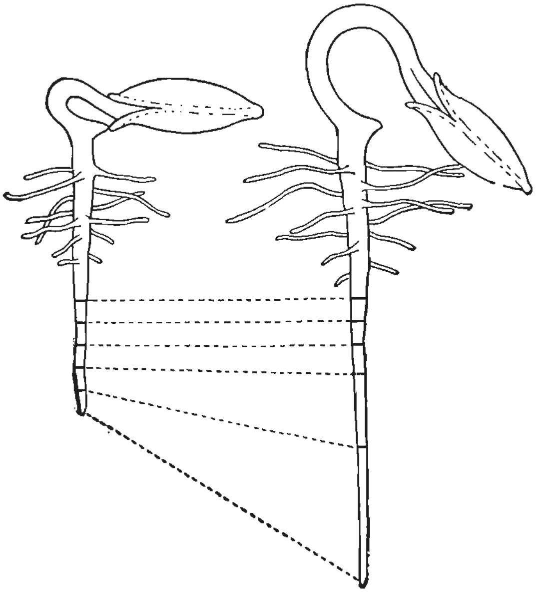


FIG. 82.—Growth of the root in length. Two squash seedlings, the one at the right a day or two older than the one at the left. The change in length of the zones between the markings, originally equidistant, shows that growth in length takes place only very near the tip of the root.

small mass of tissue usually not more than two or three millimeters in length, and composed of small, thin walled and richly protoplasmic cells which are capable of rapid multiplication. Behind this is the zone of growth or cell enlargement, where the cells which have been formed in the terminal zone stretch and elongate. It is in this zone (only a few millimeters in length), and here only, that growth of the root in length takes place (Fig. 82); and it is the force exerted here by cell elongation which drives the root tip through the soil. Just back of this region, in turn, is the zone of maturation, where the cells, now having attained their

full size, assume their mature characteristics. Here differentiation begins, the central cells developing into wood and phloem, those farther out into cortex, and the outermost ones into epidermal cells and root hairs. It should be noted that the width of the young root is determined by the width of the meristem,

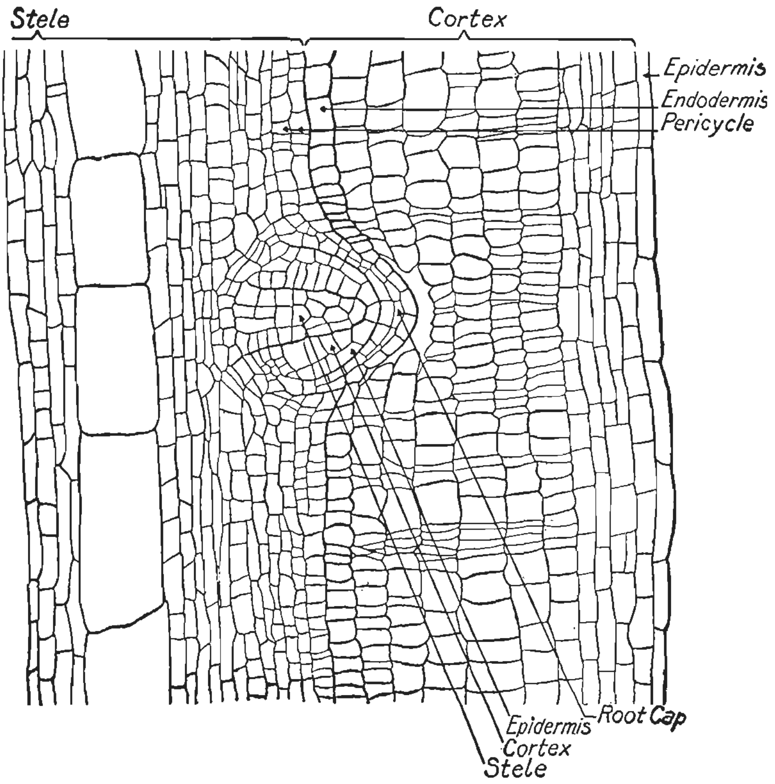


FIG. 83.—Longitudinal section through a portion of a root, showing a young lateral root developing on the outer surface of the fibro-vascular cylinder (stele) and beginning to force its way through the cortex to the outside. (*From Weaver.*)

and that no lateral growth occurs here at this time. The root grows in thickness through the subsequent activity of a cambium farther back along its axis.

Branching in the root takes place in a manner very different from that found in a stem. A lateral root, instead of arising as an outgrowth from the surface, begins with the development of a group of meristematic cells in the outer layer of the vascular

cylinder. This becomes organized as the terminal growing point of the lateral root, which now pushes out through the cortex of the old root and breaks out at its surface (Fig. 83).

The terminal growing point at the apex of a stem resembles in its essential features that of a root, but it is somewhat more complex in structure (Fig. 84). Instead of giving rise to a single organ, as in the root, it here produces both a new stem and new leaves, and often new floral organs. The stem itself increases

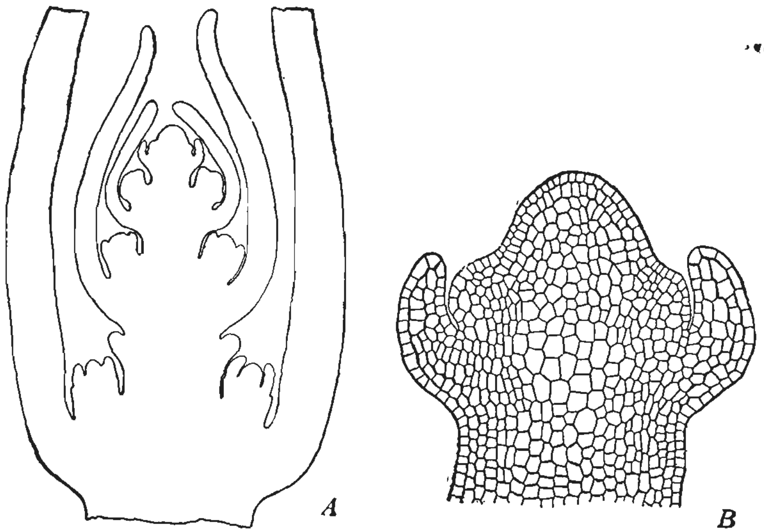


FIG. 84.—Terminal growing point of a stem. *A*, longitudinal section through the stem tip of *Salvia*, showing the development of young leaves and axillary buds; *B*, the tip of the growing point more highly magnified showing the stem apex and two leaf primordia. (*From Haupt.*)

in length much as does the root, and the leaves arise along the sides of the meristem as minute wrinkles or surface outgrowths which become progressively larger until mature size is attained. The leaf, however, is an organ of limited growth, and contains no permanent growing point of its own, although the parallel-veined leaves of monocotyledonous plants (like the grasses) may continue to grow in length for some time through the meristematic activity of the tissue at the very base of the leaf.

The growing tip of a stem, with the adjacent leaf rudiments, is known as a *bud*. Branches of the stem arise through the development of lateral buds, most commonly in the leaf axils, and these include representatives of all the tissues rather than

proceeding from the vascular cylinder alone, as in the root. Most buds, particularly those which are in a dormant state, are protected by bud scales.

The differentiation of the organs and tissues within the bud often takes place very early. In the winter buds of most woody plants, for example, the leaves for the next season's growth are all present and their arrangement and shape are well established, though the internodes of the stem of course are extremely short. As to what a bud shall be—whether, for example, it shall contain leaves or flowers—is determined during the preceding summer, when the bud begins its development. As the bud commences to grow in the spring, these performed organs merely increase in size.

In the elongation of the stem the zones are by no means so well marked as in the root, and their combined length is greater. Most of the cell division is at the extreme stem tip, but some of it takes place over much of the zone of growth, which may here extend a distance of several centimeters.

Lateral Growing Point, or Cambium.—The lateral growing point is somewhat more complicated than the terminal one and its activities are often a little hard to visualize. The best example of such a meristem is the *cambium* of the fibro-vascular cylinder of root and stem, highly developed in all typical woody plants. It has been shown in the previous study of the stem (and except for the absence of a pith the root is essentially similar) that the fibro-vascular tissues are arranged in a cylinder, with a ring of wood within and a ring of phloem without (Fig. 52). Between these two rings is a very thin layer of tissue, in its resting period often only one cell in width, which is formed of the same small, thin walled, and richly protoplasmic cells which are characteristic of terminal growing points. This is the cambium, and by its activity the fibro-vascular cylinder, and thus the whole stem, grows progressively stouter. Unlike the one-sided terminal meristems, however, this lateral growing point adds to the tissues *on both its sides.* When the cambium is active and cell division is taking place, the newly formed cells which lie on the inner edge of the cambium, next the wood, undergo a period of enlargement and maturation and become the outermost wood cells; and the new cells which lie on the outer edge of the cambium, next the phloem, similarly develop into the intermost phloem cells; but a zone of thin walled "embryonic" tissue still remains

between the two (Fig. 85). Thus the cambium, never growing itself, continually adds to the thickness of both its adjacent tissues. The cambium cells are very long in proportion to their width, and the formation of new longitudinal walls, when these cells divide, is markedly different from this process in ordinary tissues (Fig. 86).

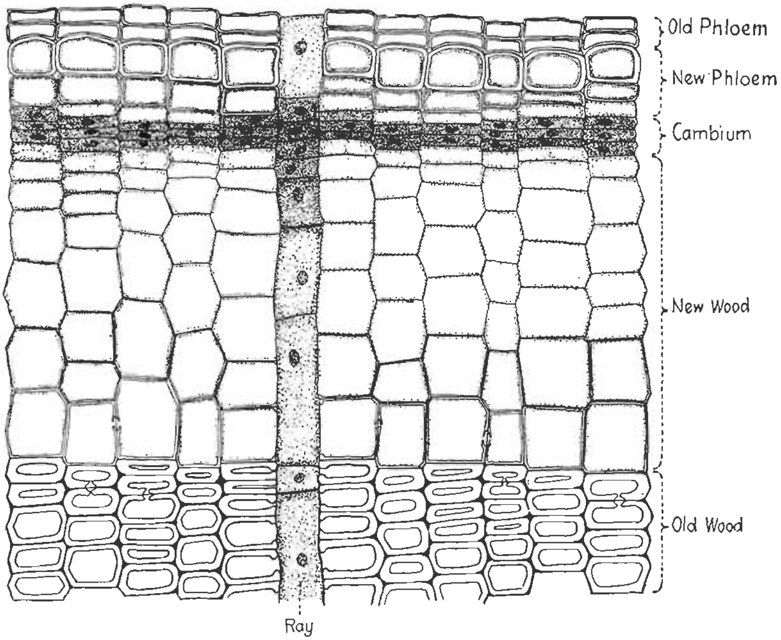


Fig. 85.—Cambium of pine stem actively producing new wood and phloem. The cambium is densely filled with protoplasm. The youngest cells of wood and phloem, lying next the cambium, are still small, but as they grow older they soon expand to their mature size. The new wood cells are still very thin-walled and retain a lining of cytoplasm, which later disappears entirely.

Just as the terminal meristem is carried out by the growing root or stem tip, so the cambium ring is carried farther and farther away from the center of the stem by the growing wood; and the phloem, lying outside the cambium, is also carried out, not alone by this growth of the wood but by the increase in its own thickness which has taken place at its inner edge (Fig. 87). Cambial activity perhaps may be crudely pictured by comparing it to the growth of a wall of brick (the wood) surmounted by a coping of tile (the phloem); and by assuming that just at the junction

between brick and tile a bricklayer (the cambium) is able repeatedly to insert bricks and tiles, the wall thus mounting upward and carrying an ever-thickening coping of tile on its top.

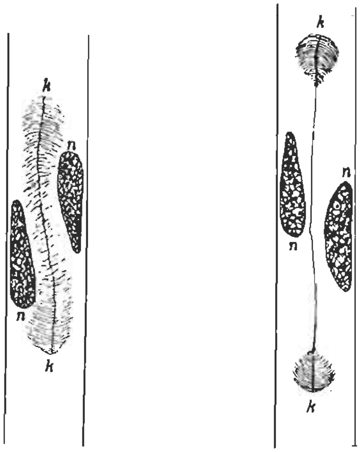


FIG. 86.—Stages in the division of a cambium cell showing the peculiar method of formation of the new cell wall in these elongated cells. *n*, nucleus; *k*, kinoplasmasome, through the activity of which the new wall is laid down. (*From Bailey.*)

As a consequence of this method of growth, the youngest layers of the wood are the outermost and the youngest layers of the

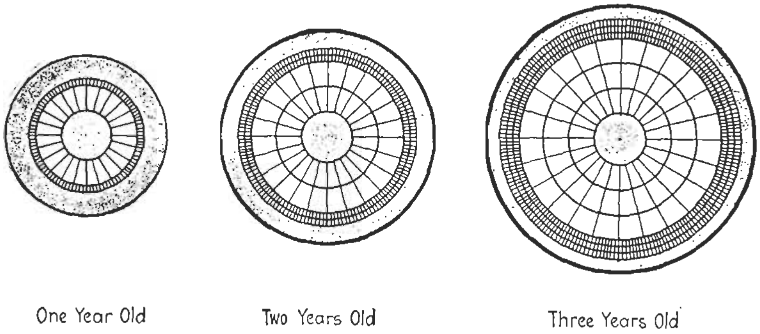


FIG. 87.—Growth of a stem in width (diagrammatic). Transverse section of three progressively older stems. Through the activity of the cambium a new layer of wood and of phloem is added each year. Pith and cortex dotted, wood plain, phloem lined.

phloem are the innermost; and the past history of these two tissues, as it is preserved in their structure, should thus be read in opposite directions. In woody plants, where growth in thickness

is considerable and continuous, the phloem, because of its rather delicate texture and the strain which is put upon it, becomes much stretched and crushed in its outer layers. These ultimately are sloughed off with the bark, whereas the wood, with its much firmer structure, remains unchanged. Well marked growth rings are developed in the wood so that an inspection of this tissue as seen in cross section makes it possible to read with much accuracy the age and past history of the plant.

Cork Cambium or Phellogen.—Another lateral growing-point of importance is the *cork cambium* which produces the layers of corky bark. This may arise almost anywhere in the cortex or in the old phloem, and develops on its outer face a row of corky cells which soon die and constitute the waterproof layer characteristic of bark tissue (Fig. 55).

A cambium occurs universally in stems and in roots where continued lateral growth takes place, and extends the full length of both organ systems, merging into the terminal growing points of the stem on the one hand and of the root on the other, and thus connecting the two by a layer of meristematic tissue.

Primary and Secondary Tissues.—The tissues laid down by a cambium are often rather regular in the arrangement of their cells, particularly in species where all the cells are of approximately the same size. This is due to the fact that each cambium cell has produced a whole row of wood cells within and of bast cells without, and that these cells naturally are arranged in a straight line along the radius of the stem passing through the cambium cell which is their common ancestor (Fig. 85).

Tissues produced by a cambium are known collectively as *secondary* tissues, and they all display in transverse section this regular arrangement of their cells. *Primary* tissues are those which arise from a terminal growing point, and in transverse section their cells are likely to be arranged irregularly, the regularity here, however, being conspicuous in longitudinal sections (Fig. 81). The epidermis, cortex, and pith, and the first formed wood and phloem, all are primary in their origin. The great bulk of the wood and phloem in woody plants, together with the corky bark, are all secondary.

Differentiation.—Growth is not mere increase in size but gives rise to definite organs and organ systems, which are markedly different in shape, structure, and function. This *differentiation* is ultimately due to the fact that growth does not occur at the

same rate in different parts of the plant; that cell enlargement, both in amount and in direction, differs in different tissues and produces cells of diverse shapes; and that in maturation the cells undergo specific types of development. What causes and controls differentiation of the plant body as growth takes place is not well understood. Much of it doubtless is due to the hereditary constitution of the plant itself, though environmental factors are also important. One region or organ of the plant, if used as a storage reservoir, may actually decrease in size while the rest of the plant is growing. The development of certain organs is also dependent on the fulfillment of rather definite external or internal conditions. In most perennial plants, for example, the reproductive structures (flowers and fruit) develop only after the plant has succeeded in accumulating an ample supply of reserve food from which they may be built. Whatever stimulates very rank growth of the vegetative parts, such as an abundance of water and nitrate salts, will tend to retard the development of floral organs; and conditions of the opposite sort (provided a sufficient supply of reserve food is at hand) will favor reproduction. The amount of photosynthetic activity, governed chiefly by the number of hours of sunlight available per day, also has an important influence on the appearance or suppression of the reproductive structures. By skillful manipulation, the growth and differentiation of the entire plant may thus to a certain degree be brought under control.

Growth in one organ or region is often definitely correlated with growth in another, so that the entire individual seems to be closely knit together in development. The relative sizes of the root system, the stem system, and the leaf system, for example, remain essentially constant as the plant grows, and the removal of any of these organs will result in a *regeneration* of similar ones until the balance is restored. Thus a tree which has been defoliated by insects will grow a new set of leaves; and a stem, cut off and placed under proper conditions, will form a new root system. Such growth correlations may be due to nutritional factors, to the production of specific formative substances, to the operation of hormones, or to the transmission of protoplasmic stimuli from one part of the organism to another. Whatever their cause, it is evident that a knowledge of their operation must underlie all understanding of the form and structure of the plant body.

QUESTIONS FOR THOUGHT AND DISCUSSION

377. Why cannot mitosis be studied easily in living cells?

378. In what direction, or plane, with reference to the main axis of the stem are most of the cell divisions which take place at a terminal growing point? at the cambium?

379. If one wishes to count the number of chromosomes in a cell, at what stage in mitosis can he best do it, and in what plane should he cut the section of the cell?

380. What disadvantage would there tend to be in very large cells? in very small ones?

381. What is the chief difference in method of growth between animals and plants?

382. With what other important differences between animals and plants is this difference in method of growth associated?

383. The zone in which elongation occurs at the root tip is much shorter than the corresponding zone at the stem tip. How do you account for this fact?

384. Growing points of plants are usually good to eat. Why should this be so?

385. Why will the bark separate very easily from the wood of a twig in the spring but usually at no other season?

386. If a nail is driven into a tree trunk at a point three feet from the ground, what position will this nail occupy in the trunk as the tree grows older?

387. In just what part of the stem does growth of the pith take place? of the wood? of the cortex? of the phloem? of the epidermis?

388. Is the pith in a one-year-old twig wider or narrower than it is in a twenty-year old branch grown from that twig?

389. Where is the cortex in a tree trunk?

390. What important changes in the size and character of its tissues takes place as a young twig grows into a large branch?

391. Why is the bark of a tree almost always rough and cracked?

392. Why does the bark of a tree never become as thick as the wood?

393. If you are to determine the age of a tree by counting the annual rings, where in the tree should you make the count? Explain.

394. How can the annual rings in trees be used to study past climatic conditions? What cautions must be observed in doing this?

NOTE.—In grafting, a small twig (the *scion*) which has been cut from one plant is placed in close contact with a branch of another plant (the *stock*). This may be done in several ways, but in all cases the tissues of the stock and scion are both cut open and so placed that the cambium of one touches the cambium of the other (Figs. 79 and 80). If the operation is successfully performed, the stock and scion will unite through the knitting of their cambial layers and the scion will develop as a branch of the stock.

395. In the process of grafting, why is it necessary for the cambial layers of stock and scion to be in close contact?

396. After a graft has been successfully made, how does water get from the tissues of the stock into those of the scion?

397. Why is it important to use a sharp knife in grafting operations?

398. After placing scion and stock in contact, why is it useful to cover the cut surfaces with wax or a similar substance?

399. Plants which are not rather closely related to one another cannot usually be grafted together. What explanation can you suggest for this fact?

400. Monocotyledonous plants can almost never be grafted. Explain.

401. Nurserymen sometimes slit the bark lengthwise on strong and rapidly growing young stems to hasten the production of new wood. Why does this practice aid in wood production?

NOTE.—Pruning is the process by which certain twigs or branches are removed from cultivated trees to attain some desired result.

402. Why does careful pruning tend to make a tree more vigorous and healthy?

403. Why is pruning generally done in spring, fall, or winter rather than in summer?

404. How differently would you prune a tree if you desired fruit production from the way you would prune it if you desired the production of timber?

405. What is the danger in pruning a tree very severely?

406. When a branch is cut from a tree, the wound thus caused will usually heal and become covered with new tissue. How does this healing take place?

407. If a branch is cut off very close to the trunk the wound will heal over much more readily than if a stump is left projecting some distance beyond the trunk. Explain.

408. Why are rapidly growing plants more tender than slowly growing ones?

409. Why do asparagus stalks become tougher and less desirable to eat as they grow older?

410. What is the best season to train woody vines upon trellises and arbors, or to fix the permanent shape of woody plants in other ways? Explain.

411. Why are trees in exposed places permanently bent in the direction of the prevailing wind?

412. To develop large blossoms on a chrysanthemum plant, growers cut off all the flower buds but the terminal one. Why has this the effect desired?

413. If tobacco plants are "topped" (the upper part of the stem, including the small leaves and the flower cluster, being taken off when they have begun to develop), the lower leaves on the stem, which are the valuable ones commercially, will grow larger than they otherwise would. Explain.

414. Which do you think will bear fruit first, a young seedling apple tree or a scion from the same tree which has been grafted into a large tree? Explain.

415. Why does the pruning away of a part of its roots sometimes cause a tree to bear more flowers and fruit?

416. Why do many plants flower earlier if grown in pots than if grown in the open soil?

417. Why is it that apple trees and other northern fruit trees sometimes grow well in warm climates but rarely bear much fruit there?

418. Why is a moist season good for forage crops but poor for seed crops?

419. In most plants which produce bulbs, it generally takes several years before a plant raised from seed will begin to flower. Explain.

420. Why do many apple trees usually bear a large crop only on alternate years?

421. Does it pay to take good care of an apple tree on the years in which it does not bear heavily? Explain.

422. If the "leader," or vertically growing strong terminal shoot of a tree, is removed, one of the horizontal lateral branches will usually bend upward and assume the position and method of growth of the leader. To what causes may this be due?

423. Experiment shows that every cell in the plant body (at least in its young condition) probably has the power, if isolated from other cells, of growth and regeneration into an entire plant. What suggestion can you offer as to why a cell does not do this in ordinary development, instead of remaining as a constituent unit of a single individual?

424. In what respects is an animal a much more definite and highly organized *individual* than a plant?

REFERENCE PROBLEMS

95. What evidence is there that constant and specific differences exist between the individual chromosomes of a plant cell?

96. Give the chromosome number for at least ten plant species.

97. In what respects does the division of a cambium cell differ from ordinary cell division in plants?

98. What is the shape of a typical curve of growth of a plant or plant organ (a curve in which growth is plotted against time)?

99. Describe some type of auxanometer, and explain its use in the study of plant growth.

100. What are the differences between propagating plants by *cutting*, *layering*, *budding*, and *grafting?*

101. In grafted trees, does the stock have any effect on the growth and character of the branch which develops from the scion? Does the scion have any effect on the stock?

102. How are "dwarf" fruit trees produced?

103. Of what importance in plant growth and differentiation is the *carbohydrate-nitrogen ratio?*

104. Describe the phenomenon of *polarity* which often appears in the regeneration of plant structures.

105. What is the difference between the *cell theory* and the *organismal theory* of plant development?

106. Give the author and title of three important books or other scientific publications dealing with plant growth, and outline briefly the content of each.

107. Name several botanical investigators who have done important work on growth and differentiation in plants, and state the notable contributions made by each.

108. Give the derivation of the following terms and explain in what way each is appropriate:

Mitosis	Meristem
Spireme	Phellogen

CHAPTER IX

THE PLANT AND ITS ENVIRONMENT

The form which a plant assumes and the activities which it carries on are due to the combined effect of two major factors. These are, first, the *inherent characteristics* of the plant itself, determined by the specific constitution of its protoplasm and transmitted from one generation to another by heredity; and second, the surroundings or *environment* in which the plant lives. Plants are so diverse and environments so varied that the relations which exist between the one and the other are many and complicated. A study of these relations forms the subject matter of the science of Plant Ecology, some of the problems of which will be discussed briefly in this chapter.

It is evident that even for the same plant, growing in the same spot, the conditions of light, temperature, moisture, and various soil factors may change radically. Between two plants in different places, environmental differences may be even more pronounced. These various external factors vitally affect the way in which the plant functions, and it is therefore evident that if a plant is to thrive and maintain itself, it must be able to modify its form and activities to meet this ever-changing environment successfully. One of the most remarkable facts of biology is that organisms do possess, in greater or less degree, this characteristic of advantageous *regulation* of structure and function in conformity to the changing external world. As to what are the causes of these regulations there is much difference of opinion and no certain knowledge. In describing plant activities, most of which contribute so obviously to the welfare of the individual, one continually finds himself using terms which imply purpose or effort. It is indeed very difficult to describe the facts of form and function in simple language without tacitly assuming that there is within the plant something which directs and regulates its life so that it will tend to do whatever is to its own best advantage. Such an assumption is, of course, quite contrary to a strictly scientific attitude toward living things, which

demands for every observed change a definite physical cause and not a psychological one; and it introduces a deeper problem which is clearly the province of the philosopher rather than of the botanist. The latter should content himself with recording carefully all changes induced in the plant by a changing environment, and with analyzing as carefully as possible the factors which seem to be responsible for these changes.

Stimulus and Response.—In such a study it is important to remember that the environmental forces do not act on the plant as they would on a lifeless body—on a stone or a drop of water, for instance—merely raising its temperature, illuminating its surface, pulling it down by gravity, or affecting it in other direct ways; but, instead, that each of these forces acts as a *stimulus* which brings forth on the part of the plant a definite *response.* This response may be either a change of function or a change of structure. To the same stimulus the response of one plant may be very different from that of another, and the responses of different parts of the same plant also may differ greatly. The stimulus is merely a trigger which releases a response. Just what a given response will be depends entirely upon the constitution of the living substance of the plant itself. This characteristic trait of protoplasm whereby it is continually reacting or responding to stimuli is known as *irritability,* and is a distinctive quality of all living things. In animals, protoplasmic irritability is extraordinarily developed in nervous tissue, which receives the stimuli and controls the responses of the organism. In plants, however, no nervous system has been differentiated, and although some regions are much more sensitive than others and evidently may transmit the effects of a stimulus for a considerable distance, it is the protoplasm of the ordinary cells which is chiefly concerned in the many responses made by the plant.

It should also be noted that although mature parts of the plant, particularly those which are soft in texture, are able to change their form and position to some extent through regulating the turgidity of their cells, it is the young and growing regions which are most sensitive to stimuli and are thus best able to bring about regulatory changes of structure and position.

In any discussion of the effect of the environment one should not only consider the reaction of the individual plant, but should also look at the problem from the historical viewpoint

and study those inherited characteristics which enable it to thrive in a particular environment and which have become implanted in the species during the course of its evolution. Adjustments of this kind, either of structure or function, are usually spoken of as *adaptations*. The natural adaptations of cacti for desert life and of orchids for insect fertilization may be cited as examples.

Attention has been called to the complexity of the environment in which the plant grows. The first step in an analysis of the relations between this environment and the plant is to isolate the separate environmental factors and to study the specific effect of each. Of the wide range of such factors a few are particularly important and deserve consideration here, notably temperature, light, gravity, moisture, and various chemical substances, which constitute the *inorganic* environment; and the surrounding plants and animals, the *organic* environment. Inorganic factors which are effective through the medium of the atmosphere are termed *climatic;* those which act through the soil, *edaphic*.

Temperature.—It is characteristic of all vital processes that their maintenance is possible only within a comparatively narrow range of temperature, and temperature changes therefore elicit marked responses in the activity of protoplasm. In general, active life is possible for the higher plants between 0° and 50° C., although these limits vary much from one species to another. The lowest temperature at which a given plant can continue to live is known as its *minimum* temperature and the highest as its *maximum*. At some point between these two the plant displays its greatest activity and this point is known as its *optimum* temperature (Fig. 88).* The various physiological processes which go on within the plant, such as photosynthesis, respiration, and growth, each have their minimum, optimum, and maximum temperatures, and these are not necessarily the same for the different processes.

Members of the vegetable kingdom lack the high and delicately maintained body temperature which is characteristic of the higher animals, and the temperature of most plants follows rather closely that of their environment, absorbing heat or losing heat as the environment becomes warmer or colder. The body

* These terms *maximum*, *minimum*, and *optimum* are also used for other environmental factors, notably light and moisture.

temperature of the plant may sometimes fall a little below that of its immediate environment, owing to excessive radiation or evaporation; or it may sometimes rise noticeably above it owing to the release of heat during respiration, especially in regions where growth is active. The latter phenomenon is particularly conspicuous in the case of intense bacterial action, for the amount of heat liberated by the vigorous respiration of these lowly plants is often sufficient to raise the surrounding temperature markedly.

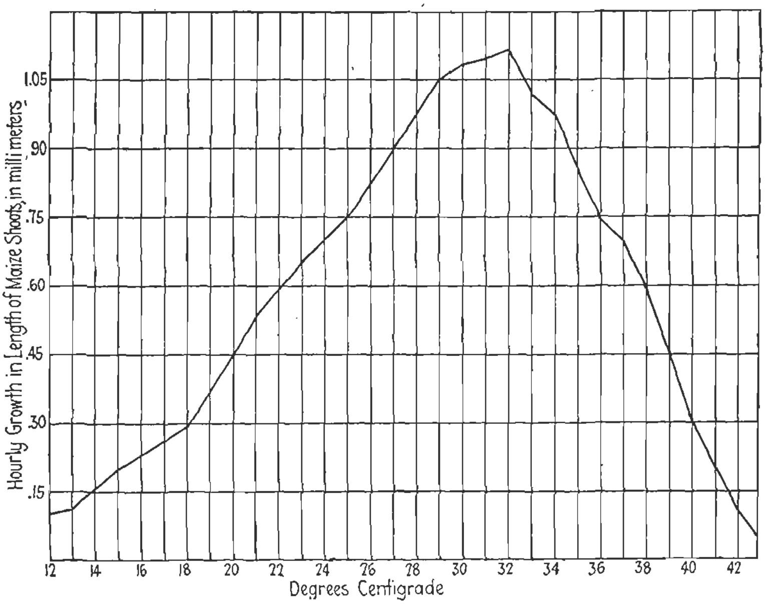


FIG. 88.—Growth in length of maize shoots per hour, when exposed for twelve hours to a constant temperature. The minimum temperature for growth was in this case found to be 12°, the optimum 32°, and the maximum 43°. (*After Lehenbauer.*)

The problem of the temperature relations of plants is further complicated by the fact that by proper treatment a plant may often become accommodated or "hardened" to temperatures higher or lower than the usual limits for the species. The resistance of plant tissues to heat and cold is dependent to some degree on maturity, for young and growing tissues are much more susceptible to injury therefrom than older ones. In general, within any particular species, the ability to withstand high and low temperatures is correlated with the amount of water in the cells and particularly in the protoplasm itself. Where water is

ınt, resistance tends to be low; where it is scarcer, resist- higher.

'e are well-marked inherited differences in the temperature ıs of plants. The optimum for an alpine plant must sly be far lower than for a native of the tropics. Certain ıave their normal habitat in the water of thermal springs ıers in the frigid arctic seas. Melons have a much higher m than peas, and some varieties of apple, peach, and re distinctly "hardier" than other varieties.

temperature of the soil is often of as much importance to nt as that of the air, for the rate of absorption of water lts depends in no small degree upon this factor. Here, herited differences are very marked; for although most will not thrive unless the soil is relatively warm, certain and alpine species are able to carry on absorption at atures almost down to the freezing point.

t.—The essential part which light plays in the life of plants through its influence upon the process of photo- sis has already been emphasized. From light rather than eat, electricity, or other sources, the plant derives the energy which it stores up in potential form in its food; this important capacity of an energy-provider light is re essential to all plants. This influence is evidently an t one, however, particularly in the case of non-green for most of these thrive in the absence of light as long as od supply holds out.

e apart from its indirect role in nutrition, light exerts direct effects, most notable of which are the growth ents made by plant parts in response to the stimulus of ation. Not all plants and not all parts of plants respond same way to this stimulus. As a general rule the stem n toward the source of light, the root away from it, and f, by the twisting of its petiole, will assume a position in he broad surface of the blade is at right angles to the light 'ig. 89). Any movement which is a specific reaction to mulus of light is known as a *phototropism.* A normal therefore said to be *positively phototropic*, a root *negatively opic*, and a leaf *transversely phototropic*, or *diaphototropic.* gh the results of phototropism are usually much more ble where a plant receives its illumination from one side t plays an important part in the orientation of plant

structures generally. The advantageous character of the ordinary phototropic responses is obvious.

Not only does light affect the position of plant organs, but it has a profound influence upon their structure. The stems of green plants grown in the dark are usually slender, much elongated, and provided with little woody tissue; and their leaves are greatly reduced in size, and undifferentiated internally. Chlorophyll fails to develop, and the plant assumes a pale yellow

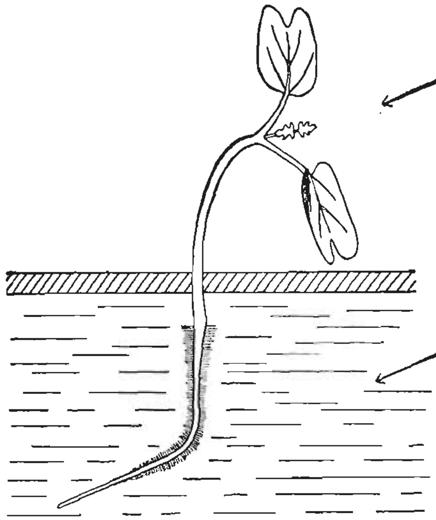


FIG. 89.—Phototropism. A mustard seedling growing with its root in water. This plant was at first illuminated from all sides, but later from only one (shown by direction of arrows). Note that the stem has bent toward the light and the root away from it, and that the leaves have taken up a position at right angles to the light.

color. This general effect of darkness is known as *etiolation* (Fig. 90), and begins to show itself whenever the supply of light falls below the optimum either in duration or in intensity. If sufficiently pronounced, etiolation ultimately results in death. The stimulus of light upon protoplasm evidently prevents the abnormal growth seen in etiolation, but how this effect is brought about is not understood.

Too little illumination is thus harmful to the plant, but too much may be equally so through its toxic effect upon protoplasm. To the blue, violet, and ultra-violet rays living substance is particularly sensitive, and in many plants the position or struc-

ture of parts may be so modified that as small a surface as possible is exposed to light when it becomes very bright. In some species,

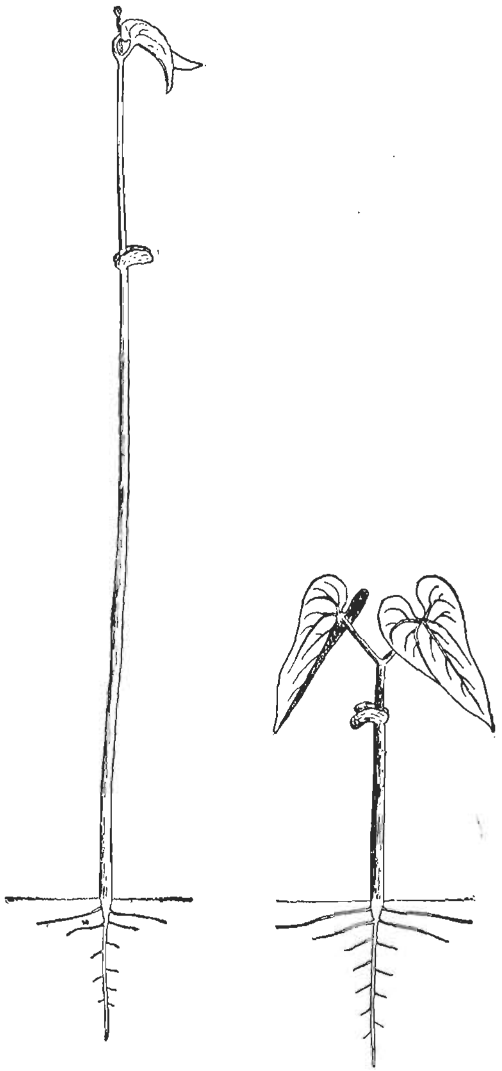


FIG. 90.—Etiolation. The two bean seedlings are of the same age but the one at the right was grown under normal illumination, the one at the left, in darkness. Note the longer internodes, the paler color, and the poorer leaf-development of the darkened plant.

for example, the broad surface of the blade is presented to light of moderate intensity, but only the edge to very bright illumination.

Toward light, as toward temperature, plants display certain inherited adaptations. Some green plants are able to thrive in light of comparatively low intensity and are said to be *tolerant* (Fig. 91), in the sense that they will tolerate a considerable degree of shade. Others will grow normally only where the illumination is good, and are said to be *intolerant* (of shade).

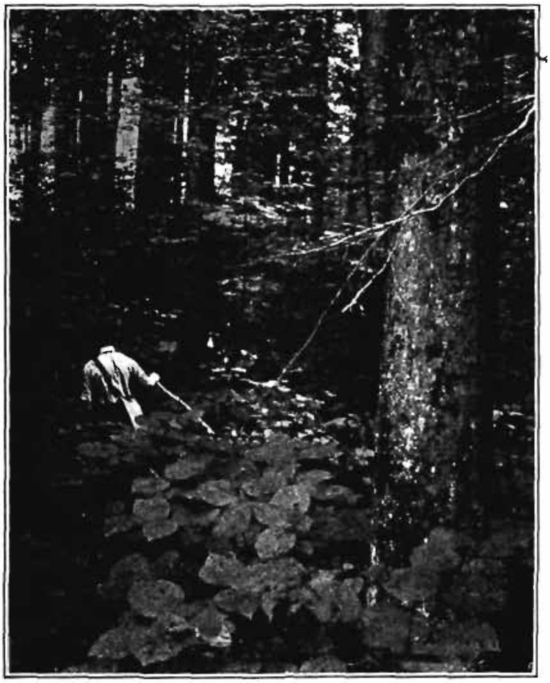


FIG. 91.—Plants tolerant of shade. These broad-leaved plants of *Viburnum* are able to thrive on the forest floor, where the lower branches of the forest trees have died from lack of light.

Some are sensitive to intense light and thus cannot live in the open, whereas others, either through the greater resisting power of their protoplasm or through various structural modifications, are able to thrive in the most brilliant sunlight. *Sun plants* in general have a thicker palisade layer in the leaf, a thicker epidermis, and a greater preponderance of stomata on the lower leaf surface than is the case in *shade plants:* and these traits not only distinguish different species but also plants of the same species, or leaves on the same plant, if grown under conditions of relatively high or relatively low illumination.

Plants also respond in characteristic fashion to differences in the length of the daily period during which they are exposed to light, a fact which is of much importance in determining the differentiation of plant structures and especially the relative development of vegetative and reproductive organs. Plants which produce flowers only when the daily light period is relatively short are known as *short-day* plants. If these are subjected to a longer daily illumination they never flower, but develop only vegetative organs. *Long-day* plants, on the other hand, will flower and fruit only when the daily light period is a relatively long one. This phenomenon of *photoperiodism* is of much practical importance to a plant grower in enabling him, through the use of artificial illumination or shade, to control the development of his plants to some extent.

Gravity.—Gravity in its effect upon plants is unlike temperature and light in that it is both continuous in action and

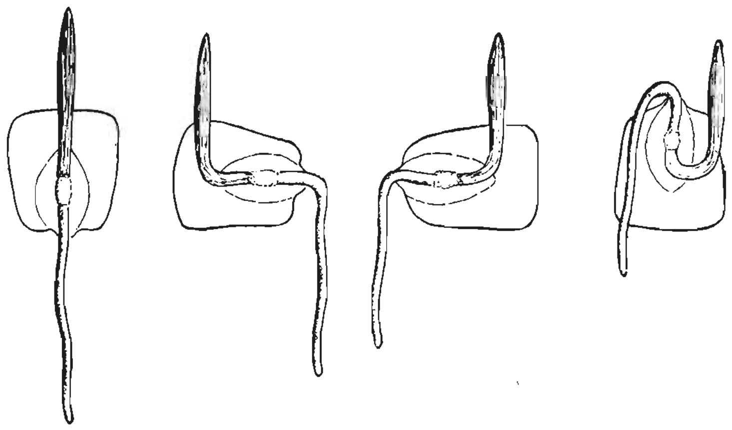


FIG. 92.—Geotropism. Four kernels of corn which have germinated in different positions. The young root in every case has grown downward and the young shoot upward.

constant in strength. It is a very important factor in determining the direction of growth in plant parts and, like light, it affects different organs in different ways. Any reaction to the stimulus of gravity is known as a *geotropism* (Fig. 92). Stems ordinarily tend to grow in a direction opposite to the force of gravity and are thus *negatively geotropic.* Primary roots and certain other portions of the root system, on the contrary, tend to grow directly toward the center of the earth and are thus *positively geotropic.*

Most leaves tend to take up their position at right angles to the force of gravity and many lateral roots also grow in an approximately horizontal direction. Such organs are said to be *transversely* geotropic, or *diageotropic.* The advantage of these specific tropisms to the plant is obvious.

Plants differ considerably in their inherited adaptations to the influence of gravity. Stems of prostrate plants have lost their negative geotropism and may even develop into rootstocks or tubers which react toward gravity like roots. The responses of flowers and fruits to this stimulus also are very diverse and for the most part seem to be advantageous to the plant.

The mechanism of stimulus and response has been studied more carefully in the case of geotropism than it has in that of other environmental factors. If very young seedlings in which the root and stem are just appearing are fixed in any position whatever, the young root will invariably grow downward and the young stem upward (Fig. 92). By attaching such seedlings to a disc and revolving it rapidly, centrifugal force may be developed which is greater than gravity, and in such a case the young plants orient themselves to this new stimulus, the roots growing outward in the direction of the force and the stems inward, in the opposite direction. The force of gravity may also be practically eliminated, without such a substitution of another and more powerful force, if the disc to which the seedlings are attached is revolved in a vertical plane by clockwork, thus exposing all sides of the seedling successively to the stimulus. Under these conditions, the root and the stem continue to grow in the direction in which they happened to start with no reference at all to gravitation. The pull of gravity, or any other force which may be substituted for it, must therefore be able in some way to stimulate the growing regions of root and stem so that growth occurs in certain definite directions. It has been proved that the very tip of the root, for a distance of approximately one or two millimeters in length, is the only portion which is sensitive to the stimulus. If this region is pointing downward, no bending of the root will take place, regardless of the position of the rest of the organ. If this region is horizontal, however, the root will bend downward until the sensitive tip itself points downward again. The actual bending never takes place in the tip, however, but always in the growth zone some distance behind it. As to how the stimulus is perceived by the tip, and how it is trans-

mitted to the zone of bending, are not certainly known. It has been suggested that the influence of gravity upon the position of starch grains or other solid bodies in the cells may be a factor, but a series of more complex physical and chemical changes are probably involved. The transmission of the stimulus may be along protoplasmic connections from cell to cell, as in nervous tissue, or it may be due to the passage of *hormones* or chemical messengers, similar to those which play such an important part in animal physiology.

Mechanical Contact.—Certain plant organs respond to the stimulation of contact with solid bodies. This *thigmotropism* is shown best by the tendrils of various climbing plants, which grow toward any object which they may touch and ultimately curve around it, in this way holding the plant body to a support. Most root tips, on the other hand, tend to grow away from a solid object, a tropism which is useful in causing them to avoid impassable obstructions in the soil.

Moisture.—Of vital importance to every plant is the maintenance within it of a sufficient supply of water, and attention has already been called to the preponderant role which this substance plays in plant activities. It comprises over ninety per cent of most living plant tissues; practically all of the physiological processes of the plant are carried on in solution within it; the transportation of substances from place to place through the plant body is accomplished by their diffusion (in solution) from one cell to another; water is one of the two essential raw materials in photosynthesis; and the normal form and proper functioning of the softer plant tissues is maintained by keeping their cells completely filled and turgid with water. It is therefore to be expected that the characteristic structures and activities of plants should be concerned with obtaining and conserving an ample supply of this valuable liquid.

Definite movements and changes of position with reference to moisture are shown chiefly by roots. The root tip is sensitive to variations in the water content of the soil, and will turn from a region of low content to one of higher. Such a response is known as an *hydrotropism* and results in the pursuit of moisture by roots for considerable distances, notably when the surface layers of the soil are drying out and the water table is descending.

It is in responses of structural change rather than those of movement, however, that the effect of moisture is most often

manifest. Plants which have access to abundant water supply grow luxuriantly, for the most part, and have relatively large leaves and soft tissues. Cuticle and epidermis are thin and parenchyma abundant. A similar plant grown where water is scanty becomes stunted throughout and has much smaller leaves. Its tissues, particularly the epidermis and cuticle, are much tougher, and the woody elements stronger and more abundant. In some instances even more profound structural changes are produced. The water buttercup, for example, when growing on

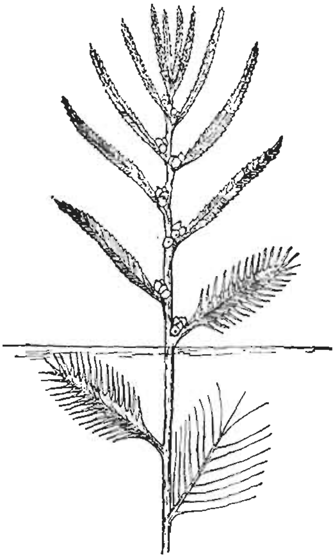


FIG. 93.—"Amphibious" plant. A shoot of mermaid weed (*Proserpinaca palustris*). Submersed leaves are finely divided, aerial leaves are undivided, and leaves between are intermediate in form.

the shore produces normal buttercup leaves, but when submersed in water develops leaves which are dissected into fine capillary segments and are thus particularly well fitted for aquatic life. Other "amphibious" plants exhibit similar structural changes (Fig. 93).

The amount of moisture in the air, through its influence on the rate of transpiration, is also of much importance as an environmental factor. It is not the actual humidity of the air but rather its *evaporating power* which is of significance to the plant. This is determined chiefly by the *relative* humidity of the air (the amount of water vapor it contains compared with

the total amount it is capable of holding, at a given temperature), the rate of movement of the air, the temperature, and the light intensity.

Xerophytes.—Inherited adaptations to abundance or dearth of water show the pronounced effects of moisture as an environ-

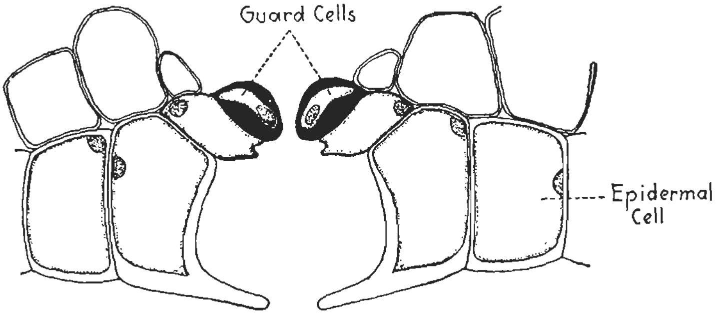


FIG. 94.—The stoma of a xerophytic plant (*Cycas*). The stoma is protected by being sunken in a pit formed by the over-arching growth of two adjacent epidermal cells.

mental factor. Many plants have become so modified during the course of evolution that they are able to thrive under conditions where the available soil water is comparatively small in amount, and where plants without special adaptive modifications would speedily perish. Such drought-loving plants are known

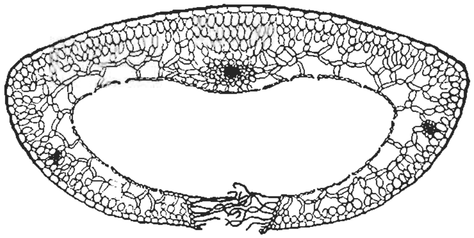


FIG. 95.—Section across the blade of a xerophytic leaf (*Empetrum*). The blade is rolled back so that the margins almost meet, thus preventing excessive transpiration from the stomata, which are on the lower (inner) surface. A felt of woolly hairs is also developed at the leaf margins which further hinders the loss of water.

as *xerophytes*, and are characterized by several types of structural and functional modifications which result in a notable ability both to draw water from the soil and to retain it in the plant tissues. The root system is very well developed in proportion to the shoot. The osmotic concentration of the cell sap is usually higher than among plants growing under less arid environ-

ments. The leaf surface is reduced, sometimes very radically; and leaves may even disappear entirely. The cuticle of stem and leaf becomes extraordinarily thick. Stomata are relatively few and are usually either sunken in pits (Fig. 94), covered with

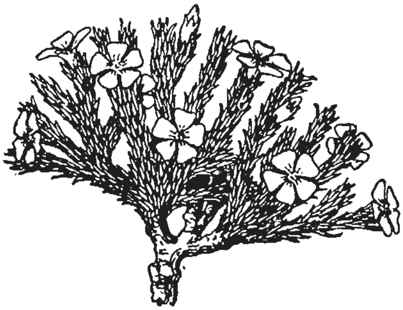


FIG. 96.—A small-leaved "cushion" xerophyte (*Silene acaulis*) characteristic of dry, alpine regions. (*From Ramaley.*)

a mass of hairs, or otherwise protected (Fig. 95). In certain cases, notably among arctic and alpine xerophytes (Fig. 96), the leaves and stems are covered with a felting of hairs. In others, particularly the xerophytes of saline soils, the vegetative

FIG. 97.—One type of xerophyte. The stonecrop (*Sedum*), showing its very thick and fleshy leaves.

organs become fleshy and succulent (Fig. 97). Internally, most xerophytes have a strong development of woody tissue.

Plants capable of growing in salt marshes, "alkali" soils, or other environments in which the soil water, although abundant,

contains such a large amount of dissolved salts that the absorption of it is more difficult than under ordinary conditions, are known as *halophytes*. This dearth of available water in their environment, although due to physiological rather than physical causes, has resulted in structural modifications similar in many ways to those of typical xerophytes.

FIG. 98.—Hydrophytes. The type with broad, floating leaves (water lily) and that with small, delicate leaves, mostly submersed (water milfoil), are both shown.

Hydrophytes.—At quite the opposite extreme from xerophytes are those plants which are adapted to live nearly or quite submersed in water. These *hydrophytes* (Fig. 98) have root systems which are much reduced or may even be entirely absent. The leaves, if submersed, are usually finely cut and dissected and *are very thin*. *Stomata are absent*. *The stems have become* very soft and weak and possess an exceedingly small amount of

woody tissue. In certain types, notably those in which the leaves (or some of them) are exposed to the air, the tissues of the plant are well provided with air passages (Fig. 99).

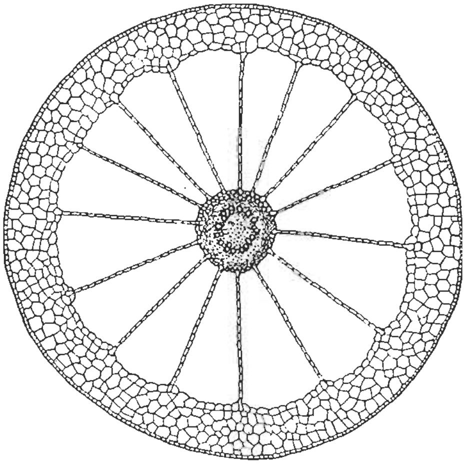


FIG. 99.—Transverse section of the stem of a typical water-plant (*Myriophyllum*). The fibro-vascular cylinder is poorly developed and the cortex is provided with large air chambers.

Mesophytes.—The majority of plant species thrive best on a moderate supply of water and are known as *mesophytes*. Living under conditions especially favorable for plant growth, they possess well developed root and leaf systems and are generally large, thrifty, and fast-growing as compared with xerophytes and hydrophytes. Their leaf area is extensive, the cuticle and epidermis rather thin, and the stomata not especially protected. Internally they are highly differentiated, particularly as to the fibro-vascular system.

Through bog and swamp plants, with their typically spongy structure, mesophytes merge gradually into hydrophytes; and at the other environmental extreme it is hard to draw a sharp line between mesophytes and xerophytes. Furthermore there are many plants, such as our deciduous trees, which are mesophytic during the summer and xerophytic during the winter. Such plants are known as *trophophytes*.

The modifications of plants with reference to their water supply are legion and provide a fascinating field of investigation, for nowhere else is the regulatory character of plant structures more clearly evident.

Chemical Substances.—The effects of chemical substances upon plants are many and far-reaching. In certain cases, particularly in the lower groups, the direction of growth or movement may be determined by chemical stimuli. Far more profound are the structural and functional changes induced by chemical substances entering the plant from the soil.

The chemical elements essential to the life of plants have been enumerated in a previous chapter. Certain of these evidently have rather specific effects on plant growth, though so many

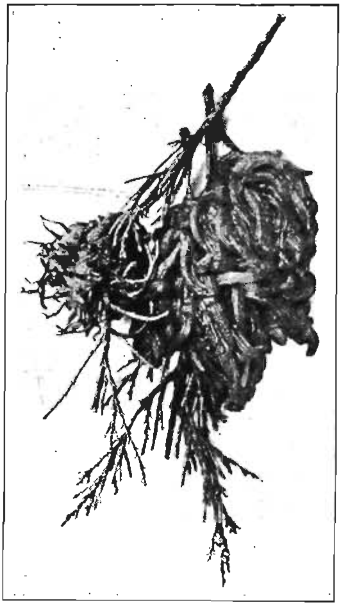


FIG. 100.—Galls produced by the attack of a fungus (*Gymnosporangium*) on red cedar.

factors are involved that an exact determination of such effects is difficult. Iron clearly is necessary for the production of chlorophyll (although forming no part of its molecule); magnesium is a necessary constituent of chlorophyll; and potassium seems to be essential for normal photosynthesis. The presence of these three elements, even though in relatively small quantities, is therefore necessary in the manufacture of carbohydrates. Phosphorus and sulphur are constituents of most proteins, and the former is especially abundant in the nucleus. Phosphorus is also believed to stimulate the development of reproductive

structures. Calcium seems to be essential to metabolism, and plays a further important part in neutralizing harmful acids, both in the plant and in the soil. Nitrogen is an essential constituent of proteins and thus of protoplasm; and when accompanied by abundant water and active photosynthesis, markedly stimulates growth, particularly of the vegetative organs. Other chemical elements seem to be essential to the activity of protoplasm, though they are needed only in very minute quantities.

Chemical substances injected into the plant body are able to stimulate growth in various abnormal ways. Notable instances of this are the great variety of galls produced on plant tissues through insect stings or fungus attacks (Fig. 100).

Plants display characteristic inherited reactions to the presence of chemical substances in the soil. Certain species, for example, thrive on saline soil where the majority of plants are quite unable to exist. Others grow only where the soil is markedly acid, and still others only where lime is abundant. Some ubiquitous types are able to exist in soils of almost any chemical composition. The distribution of plant species over the earth's surface is influenced to no small degree by their reactions to particular chemical substances in their environment.

Living Organisms.—The environmental factors which have been discussed thus far are all lifeless ones. Of the utmost significance to the plant are also the living organisms with which it is surrounded, and its relations to this organic environment are many and varied. First in importance is the struggle for survival which is taking place continually between living things; for no plant exists by itself, reacting only to the inorganic factors which surround it. It is competing with its neighbors for water, for nutrient materials, for sunlight, for insect visitors, and for other necessities. It is preyed upon by parasitic plants. It is devoured or destroyed by animals of all kinds. Only the vigorous and the fortunate succeed, and they are few compared with the many which fail and die.

Parasites.—The great majority of the seed plants are independent, deriving their sustenance directly from the inorganic environment, and the struggle between them is therefore fair combat, with victory to the most efficient. Some species, however, have abandoned this passive form of competition for active attack upon their neighbors, and have developed an ability to obtain part or all of their food directly from the tissues

of other plants. Such an organism is known as a *parasite* (Figs. 101, 102, and 103) and its victim as its *host*. The tissues of the host plant are pierced by small, modified roots, the sucking organs or *haustoria*, which grow from either the root or the stem of the parasite. These penetrate to the vascular bundles or storage regions of the host and draw therefrom a supply of manufactured

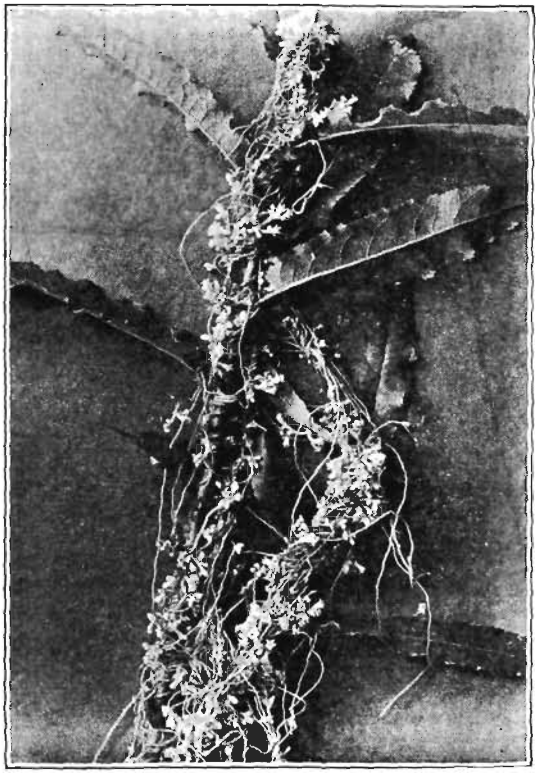


FIG. 101.—A parasite. The dodder (*Cuscuta*) parasitic on an herbaceous plant. Note the absence of chlorophyll.

food. Parasites display certain characteristic structural modifications, notably an absence or poor development of normal roots, a reduction in size of the leaves, and a partial or complete loss of chlorophyll. Some parasites, particularly those whose roots attack the roots of other plants, may be only partially parasitic, whereas others derive their entire food supply from their hosts and can live only as parasites.

The small but interesting group of insectivorous plants have gone a step further and reversed the ordinary relation between animals and plants by becoming parasites upon insects. These plants capture their prey either by a closing trap, as in the Venus's fly trap; by a pouch of liquid, as in the pitcher plants, or a by mass of sticky tentacles, as in the sundews (Fig. 104).

FIG. 102.—A parasite. The American mistletoe (*Phoradendron*) parasitic on a tree.

Once caught, the bodies of the insects are apparently digested by enzymes secreted by the plant, and may thus furnish a small supply of nitrogenous food. Parasitism is comparatively rare among seed plants but is very common in the fungi, many of which attack the tissues of both plant and animal hosts, and produce serious bacterial and fungous diseases.

Saprophytes.—Similar in certain respects to parasites are a group of plants which also depend upon other organisms for food

instead of manufacturing it independently from raw materials. This group, however, does not attack living animals and plants,

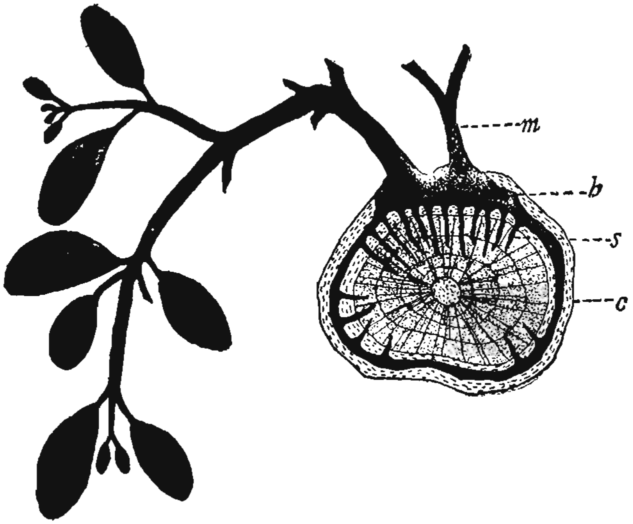


FIG. 103.—Cross section of a branch infested with mistletoe. *m*, mistletoe shoot; *h*, haustorium or organ of attachment; *s*, sinker, penetrating the host tissue; *c*, cortex of host. (*From Heald.*)

but lives instead upon their dead bodies, drawing therefrom the already combined organic compounds and using them directly

FIG. 104.—An insectivorous plant, the sundew (*Drosera*). In the sticky tentacles of its leaves, insects become entangled.

as food. Such plants are known as *saprophytes*. Here belong the bacteria of decay and all other fungi which are not parasites. There are a few saprophytes among seed plants, of which the

Indian pipe (Fig. 105) is perhaps the best known example. The structural modifications of such forms in general are similar to those which distinguish parasites. The ability possessed both by parasites and by saprophytes to use complex organic substances directly is nearly or quite lacking among ordinary green plants, which are able to absorb through their roots only simple inorganic salts.

FIG. 105.—Saprophytes. The Indian pipe (*Monotropa*).

Epiphytes.—A third type of relationship between one plant and another, and one which is usually free from destructive consequences, is presented by those species which grow upon the bodies of other plants but are not parasitic thereon. Such plants are known as *epiphytes* (Fig. 106) and are especially common in dense tropical forests. Many ferns and orchids display this habit of growth. The roots of epiphytes have no connection with the ground and do not enter the living tissues of other

plants, and in consequence they are often modified to draw moisture directly from the rain and dew. Structural features characteristic of these plants are a much thickened cuticle, protected stomata, and fleshy stems and leaves.

FIG. 106.—Epiphytes growing on a tree-trunk.

Symbiosis.—In the relationships between the plant and other organisms in its environment thus far mentioned, the advantage has been one-sided. There are instances, however, of true *symbiosis*, an intimate relation between two plants, or between a plant and an animal, where the advantage, to some extent at least, is mutual. An example of this is provided by the whole group of Lichens, each member of which is a composite organism produced by the close association of an algal species and a fungus species (Fig. 203), and in which both seem to derive a certain amount of benefit from the union. The mycorhizas, or associations between a fungus and the root tip of a higher plant, which have been mentioned in a previous chapter, are evidently other examples of the same state, as is probably the connection between the nitrogen-fixing root-tubercle bacteria and the leguminous plants in which they live. There is evidence, however, that in many of these cases of supposed symbiosis one of the partners derives so much more benefit than the other that the relation

is probably more accurately described as parasitic than as symbiotic in character.

Among the higher plants there appear many instances of relationship between organisms which are also of advantage to both, though they are not intimate enough to class as true symbioses. Most notable are those between flowering plants and insects, whereby the plant derives the benefit of cross pollination and the insect a supply of nectar; and the numerous cases where fruits are attractive to animals by furnishing them with food, and in turn are distributed widely by these animals, with consequent benefit to the plant species. These two types of relationship are very numerous and fascinating, and have long been the subject of investigation by botanists. They will be described more fully in a later chapter.

Plant Associations.—In their reactions to external conditions, different plant species either may respond in such a way as to become adapted successfully to the same general environment or may become more or less interdependent upon one another, with the result that these various species, often including plants widely diverse in size, structure, and relationship, may thus grow side by side together and form an easily recognizable group. Such a group is known as a plant Community or Association, and may be characteristic of a swamp environment (Fig. 107), a desert environment (Fig. 108), a mesophytic forest environment (Fig. 91), a sea beach environment, and many others. Each has a characteristic species or group of species which give the association its name, so that one may speak of a spruce-balsam forest association, a willow-birch thicket association, a *Poa-Rumex-Lathyrus* association, and so on.

Most plant associations are not static and constant in extent and character, but tend to expand their range to cover the entire environment to which they are well suited. Their presence may in time alter conditions so that a very different group of species ultimately supplants them. Climatic and topographic changes of various sorts may also modify conditions in time so that there may be marked changes in the distribution of plant associations. In a given locality one group of plants may thus encroach upon another. Such a *succession* may be relatively rapid, or it may extend over many years, and it will continue until stability is attained through the appearance of a vegetation which is essentially permanent. This is spoken of as the *climax* association for

the region in question. Thus in old fields in northern New England, once cultivated but later abandoned, crop plants

FIG. 107.—A swamp association. Note the contrast between the plants which compose this plant association and those in Fig. 108.

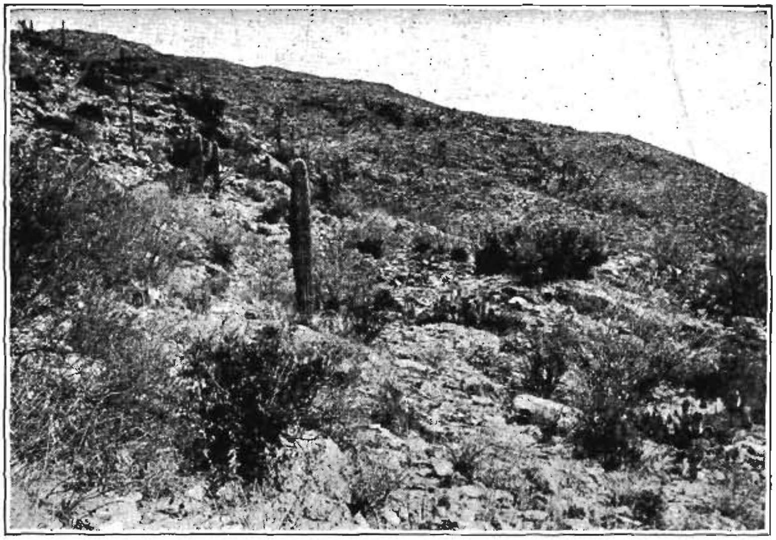


FIG. 108.—A desert association, composed of cacti and other extreme xoerphytes. (*Courtesy of D. T. MacDougal and Forrest Shreve, Desert Laboratory, Carnegie Institution.*)

were succeeded by annual herbs, either weeds or native plants; these by perennial herbs; these by shrubs of various species; these

by small and short-lived trees, like the old-field birch; these by oaks and hickories; and these ultimately by maples and hemlocks,

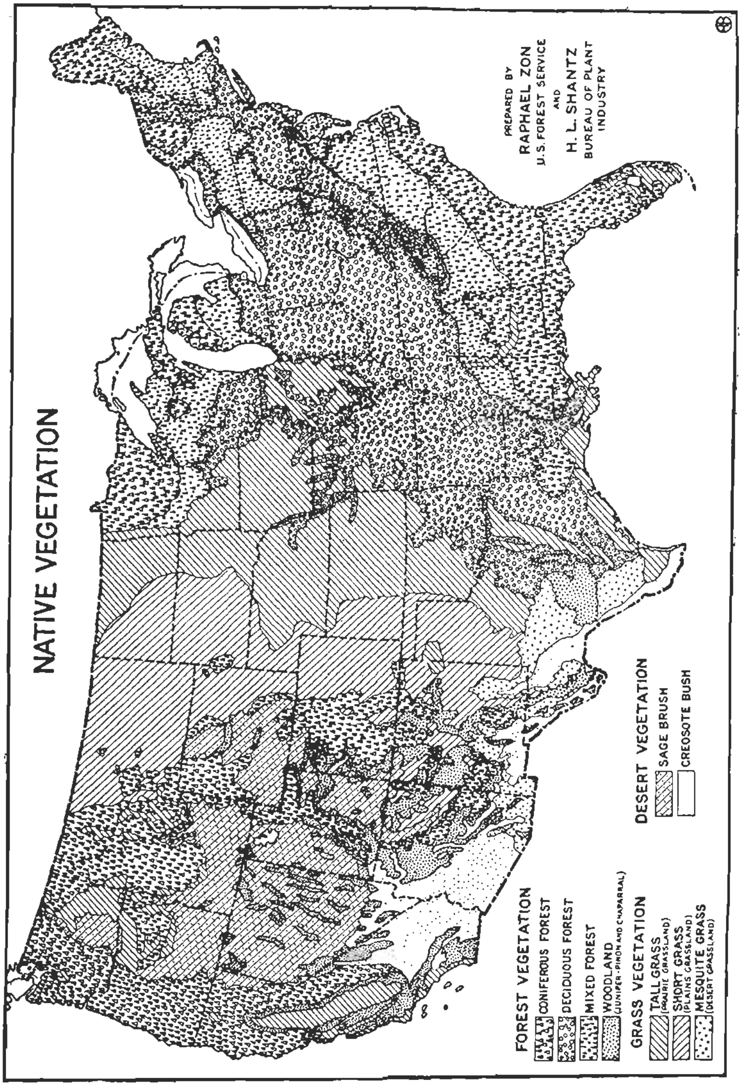


Fig. 109.—Map showing the main regions of native vegetation in the United States. (*Courtesy United States Department of Agriculture.*)

the last being the typical climax vegetation of the region. A study of plant associations and their history is an important part of ecology (Fig. 109).

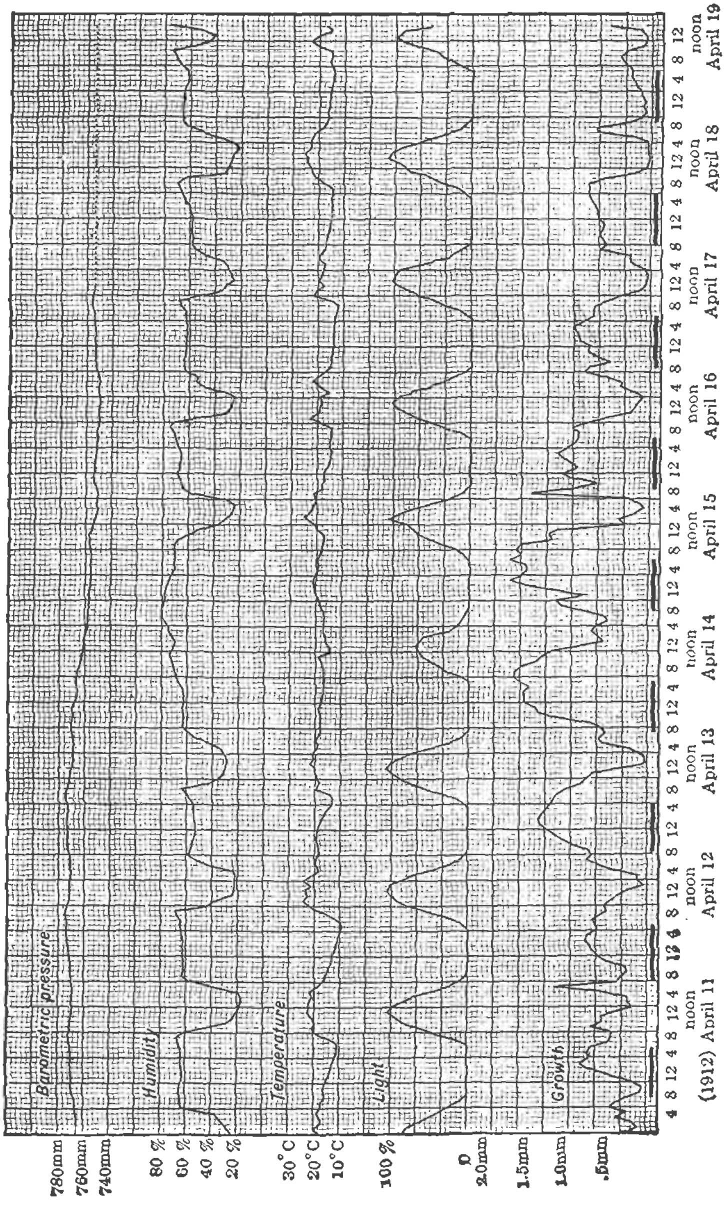


FIG. 110.—Graph showing the hourly rate of growth of a flower-stalk of grape hyacinth, and its relation to several important factors in the environment. (*From Ganong, "The Living Plant," Henry Holt and Co.*)

In this brief discussion of the influence upon plants of the various factors in their environment, there have been outlined only certain of the more important aspects of the problem which underlies the whole science of ecology. No environmental factor is paramount, and the reaction of the plant is to the whole series of them (Fig. 110). The direction of growth, for example, may be influenced both by gravity and by light, and the result is determined by the relative strength of these two stimuli under the particular conditions existing in a given case. In the same way, the distribution of a given plant species over the earth's surface is determined not alone by soil conditions or moisture or temperature or parasites, but by the whole series of environmental factors taken together. The essential point to remember *is that the structure and activities of any plant are not controlled* entirely by either the environment in which it lives or the specific and inborn characteristics of its protoplasm, but are results of an interaction between these two forces. Plants belonging to different species will develop and function very differently even under environments which are identical; and plants entirely similar will become very different if grown under different environments.

QUESTIONS FOR THOUGHT AND DISCUSSION

425. Give an example of the response of a plant to its environment which is regulatory in character.

426. What is meant by saying that "no nervous system has been differentiated" in plants?

427. From its structure, which of the tissues of the plant do you think might serve most readily as a means of transmitting stimuli quickly from one part of the plant to another, in somewhat the same way as do the nerves of an animal?

428. What structures in the plant most closely correspond to the sense organs of an animal?

429. Given an example of the "adaptation" of a plant species to the environment in which it lives.

430. What danger may there be for a species in becoming very closely adapted to a particular environment?

431. Why is a slight frost in fall or spring often more disastrous to woody plants than very much lower temperatures in the middle of the winter?

432. Why will a warm period in mid-winter sometimes result in the absence of fruit upon a tree the next season?

433. An orchard of such fruit trees as the peach, which are rather susceptible to cold, will survive better if grown on a hilltop or on the north slope of a hill than if grown in a valley. Explain.

434. Of what advantage and of what disadvantage is snow to vegetation?

435. Many of the higher animals can thrive and function normally in the winter, whereas plants cannot. To what physiological difference between the two groups is this due?

436. Of what advantage to the plant are the phototropic reactions which it displays?

437. Since most stems are positively phototropic, why is it that all the trees in the northern hemisphere are not bent toward the south?

438. Flowers are generally positively phototropic and fruits negatively so. Of what advantage are these reactions in the process of reproduction?

439. When nurserymen grow seedlings of forest trees, they often cover the plants with a lattice-work screen for the first few years. Explain.

440. Of what advantage to the plant are the geotropic reactions which it displays?

441. Most primary roots are positively geotropic, but the lateral roots which arise from them are usually transversely geotropic. How do these reactions facilitate the absorption of materials from the soil by the root?

442. Give an example of a stem which is not negatively geotropic.

443. Give an example of a root which apparently shows no definite geotropism.

444. How different is the direction in which the trunk of a tree will point if it is growing on a steep hillside from that in which it will point if it is growing on level ground?

445. How differently does gravity produce its effect when it causes a root to grow downward and when it causes a horizontally placed piece of wood, or other dead object, to bend downward?

446. Of what advantage to the plant is it to have its roots positively hydrotropic?

447. Why do desert plants usually have a highly concentrated cell sap?

448. Crocus, narcissus, and tulip plants flower and grow in early spring and by late spring have withered, not to appear above ground till the following year. For what sort of a climate are such plants well adapted?

449. Why are arctic and alpine plants xerophytic, even though there is plenty of moisture in the soil where they are growing?

450. The leaves of many evergreens, such as juniper, are pressed against the stem in winter but loosely spread in summer. Explain.

451. The timber-line (or line above which trees will not grow on a mountain side) is generally higher on a mountain range than on an isolated peak, and in ravines than on ridges. Explain.

452. The "rosette" habit of growth, where all the leaves are in a circle close to the ground and a stem is absent, is common in cold and in arid regions. Explain.

453. Why are mesophytes "generally large, thrifty, and fast-growing as compared with xerophytes and hydrophytes"?

454. Why should nitrates and potash be applied to crops such as beans and corn early in the growth of the plants, but be withheld during later growth?

455. What different treatment, as to soil fertility and moisture, should be given such crops as celery and lettuce, from that given beans and corn? Explain.

456. Why is a plant association often a very heterogeneous group, consisting of trees, herbs, saprophytes, climbers, and other types?

457. How may a knowledge of the native vegetation of a region be useful in predicting what kinds of cultivated plants will grow well there?

458. What are the advantages and the disadvantages to a plant of a parasitic habit of life?

459. How is a parasite able to withdraw food and water from its host plant?

460. Which type of plant probably appeared first in evolution, the saprophyte or the parasite? Give reasons for your answer.

461. What important rôles do saprophytes play in the economy of nature?

462. Why are epiphytes more common in dense tropical forests than elsewhere?

463. Of what value to a pine tree is its pitch?

464. What various ways can you think of by which plants protect themselves against being eaten by animals?

465. Give at least three reasons why plants which are crowded together do not grow as well as those having plenty of room.

466. What barriers hinder the dispersal of marine plants?

467. What various reasons can you suggest for the fact that some plant species are much more widely dispersed than others?

468. There are many more species of plants in the tropics than there are in temperate regions, although the number of individual plants is probably not very different. Explain.

469. As a general rule, a breed of livestock can be employed in agriculture over a much wider area than can a variety of cultivated plants. Explain.

REFERENCE PROBLEMS

109. When plants are "hardened" so that they can withstand lower temperatures, what physiological changes do they commonly undergo?

110. What is the *statolith* theory of geotropism?

111. What is a *clinostat* and of what value is it in physiological investigations?

112. What explanations have been advanced as to the method of transmission of the stimulus in the leaves of the sensitive plant, *Mimosa?*

113. Describe the investigations and conclusions of Professor Bose as to stimulus and response among plants.

114. What is the *circumnutation* shown by many growing stem tips and of what advantage is it to the plant?

115. Describe the differences between the *sun leaves* and the *shade leaves* often found growing on the same plant.

116. What effects on plant tissue have been found to result from exposure to X-rays and to radium emanations?

117. The mean annual ("average") temperatures of England and of New England are not very different, but many delicate plants will grow in the former region which will not in the latter. Explain.

118. Compare the United States and the British Isles as to rainfall and temperature during the growing season. How do these figures explain the facts that grass grows so much better there than here, and that corn grows so much better here than there?

119. Although a much wider range of plants can be grown in northern Europe than in the northern United States, the latter region has far more native species than the former. Explain.

120. Describe briefly the character of the various major plant formations of the United States shown in the map on page 206.

121. Give the author and title of three important books on plant ecology, and outline briefly the content of each.

122. Name several botanical investigators who have done important work in ecology, and state the notable contributions made by each.

123. Give the derivation of the following terms and explain in what way each is appropriate:

Phototropism	Etiolation	Parasite
Geotropism	Xerophyte	Saprophyte
Hydrotropism	Hydrophyte	Epiphyte
Chemotropism	Mesophyte	Symbiosis

CHAPTER X

REPRODUCTION

Thus far the plant body has been studied as an *individual,* in which roots, stems, and leaves develop characteristically, and function in such a way that the successful existence of the plant is assured. The individual ultimately disappears, however, and it obviously is necessary, if the *species* to which this belongs is to survive and maintain itself, that some means be provided for insuring a constant succession of new individuals, transmitting the life of one generation to the next. This is accomplished by the process known as *reproduction*, whereby the plant, by one means or another, produces a group of offspring. The structures and functions of all plants may thus be divided into two rather sharply marked groups: the *vegetative,* centering around the root, stem, and leaf, which are concerned primarily with the life of the individual plant; and the *reproductive*, centering around the flower, fruit, and seed, which are concerned primarily with the maintenance of the species. It is the latter group which will be discussed in the present chapter.

There are two main types of reproduction, markedly different from one another. These are *asexual* or *vegetative* reproduction, in which portions of the body of the parent become detached from it and are set apart as new individuals; and *sexual* reproduction, where there is a union between two specialized reproductive cells or *gametes,* from which union a new individual arises.

Asexual Reproduction.—The simplest type of asexual reproduction consists in the division of the parent plant into two or more parts, each of which becomes independent. It is a characteristic property of most plants that a small portion of the body (particularly if it includes a bud), when removed and placed under favorable conditions, will replace the missing parts and develop into a new individual. This readiness for multiplication is made use of extensively in the various arts of plant propagation, by which new individuals are produced through layerings, cuttings, and like processes. In a somewhat similar manner, a

bud or twig from one plant may be united so intimately to another by budding or grafting that it thrives and grows as an integral part of the plant to which it has been transferred. By use of these methods of artificial reproduction the horticulturalist succeeds in producing enormous numbers of individuals from a single plant. One particular advantage of such a procedure is that it insures a high degree of uniformity among the offspring, since each one of them in fact is a portion of the original individual. All true Concord grape vines or Baldwin apple trees, for example,

FIG. 111.— Asexual reproduction in the strawberry. Creeping stem (runner or stolon), some of the buds of which develop into branches which take root and ultimately form new plants. (*From Haupt.*)

are simply detached parts of the original vine or tree in which the variety originated.

In many plants, reproduction of this sort is a constant accompaniment of the slow spread and dispersal of the vegetative parts which is continually taking place (Fig. 111). Thus a grass plant may become established in one spot and gradually extend its area until it forms a considerable patch of turf. Portions of this, through accident or decay, become separated from one another, and a colony of plants takes the place of a single individual. In a somewhat similar fashion the beech tree multi-

plies itself, suckers arising from buds on the roots of the parent tree until it is surrounded by a grove of beeches, though this particular method of reproduction is not very common among the seed plants. The tips of arching branches may come in contact with the soil and root there, as often happens in the case of the raspberry. Rapidly growing rootstocks, like those of quack grass, may be very important means of dispersal and reproduction. Under suitable conditions new plantlets may even develop on leaves, as in the commonly cultivated greenhouse plant *Bryophyllum*, and in the propagation of begonias.

In many species structures have arisen which are particularly adapted for establishing new individuals by vegetative means. Here belong the *runner* or *stolon* of plants like the strawberry; the specialized axillary buds of such species as *Lilium bulbiferum*, which drop to the ground and start new individuals; and the tuber of the potato, which is a short and much thickened underground stem from the buds of which new plants arise. The bulb, as in the onion and hyacinth, and the corm, as in the crocus, carry the plant over from one season to the next (Fig. 73), and their buds ultimately give rise to a group of new plants.

Sexual Reproduction.—Far commoner and more important than the asexual or vegetative method of reproduction, however, is the *sexual.* The essential feature here is *the union of two specialized sexual cells, or gametes, to form a single cell, the fertilized egg or zygote, from which a new individual develops.* A successful consummation of this process is the function of a great variety of reproductive structures throughout the plant kingdom. These in the higher plants are called the flower, fruit, and seed. It still is uncertain as to what notable advantage is gained through this process of sexual union which should make it so common among plants. There is evidence in some cases that an increase in vigor characterizes the offspring from it, and the increased variability which often results from this type of reproduction has also been regarded as advantageous. Many very successful species exist, however, which now depend wholly or in large part upon asexual reproduction.

In the present discussion only the higher seed plants will be considered, a study of reproduction in the lower members of the plant kingdom being reserved for later chapters.

The Flower.—Seed plants are characterized by the possession of a rather complex reproductive apparatus known as the *flower.*

This consists typically of those structures directly concerned with the development of the sexual cells, together with others which contribute indirectly to the process of reproduction (Figs. 112 and 113).

Evidence from various sources indicates that the flower is essentially a short and compact branch which has ceased growing in length, and which bears lateral appendages believed to repre-

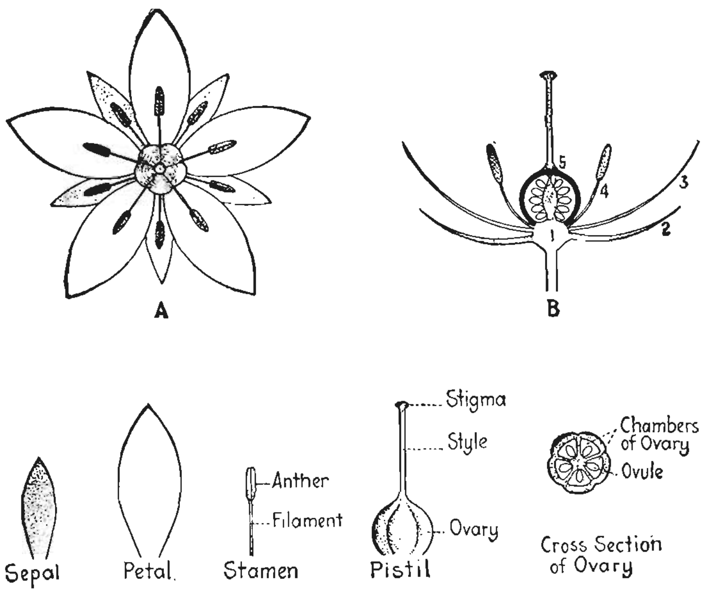


FIG. 112.—The structure of the flower of a dicotyledonous seed plant (diagrammatic). *A*, face view of the flower, showing its calyx of five sepals, its corolla of five petals, its ten stamens, and its pistil. *B*, longitudinal section, showing the relations between the parts. 1, receptacle. 2, calyx. 3, corolla. 4, stamen. 5, pistil, with ovary cut lengthwise.

sent much-modified leaves. These are so highly specialized for various functions connected with reproduction, however, that their resemblance to ordinary foliage has been almost entirely lost.

The flower stalk is merely a stem modified for the particular function of supporting the flower in a favorable position for pollination. When it bears a single flower, or is the main stalk of a cluster of flowers, it is known as a *peduncle*. In flower clusters the individual stalks are called *pedicels*. The flower develops as a branch from a bud, growing in the axil of a leaf;

and this leaf, known as a *bract*, is usually much reduced, though sometimes flowers arise in the axils of ordinary foliage leaves.

A typical complete flower consists of four circles of parts—the *calyx* on the outside, immediately followed by the *corolla*, both concerned only indirectly with the process of reproduction; and within these the *stamens* and the *pistils*, in which are developed the male and female sexual cells from the union of which

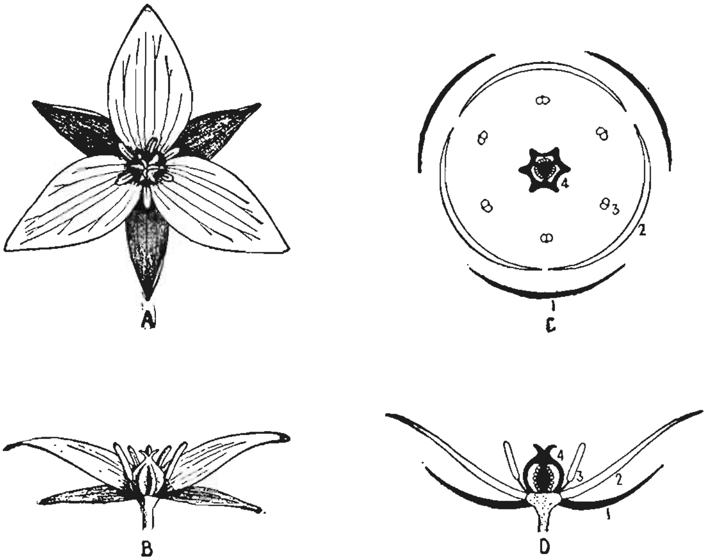


FIG. 113.—The structure of a flower of a monocotyledonous seed-plant (*Trillium*). *A*, face view of the flower showing calyx of three sepals; corolla of three petals; 5 stamens; and the pistil. *B*, side view of the flower with one petal and one stamen removed. *C*, a transverse diagram of the flower, the sepals and ovary walls black, the petals, stamens and ovules outlined. *D*, a longitudinal diagram of the flower. 1, sepal. 2, petal. 3, stamen. 4, pistil.

the new individual develops. All these structures are attached directly or indirectly to the *receptacle* or enlarged end of the flower stalk.

Calyx.—The outermost circle, or calyx, consists of units, the *sepals*, floral leaves which in most cases still retain their green and leaf-like appearance. They often are somewhat tough in texture, and function chiefly in the protection of the inner and more delicate floral structures as these develop in the bud. In some cases they may become petal-like.

Corolla.—Within the calyx is the corolla, consisting of a circle of broad, foliaceous structures, the *petals*. In their attachment

these usually alternate with the sepals, but are markedly different from them in being much more delicate in texture and of some other color than green. The chief function of the petals is to attract to the flower those insects useful in effecting pollination. This is accomplished either by conspicuous colors or attractive odors, which guide the insect to the flower; and by the secretion of a sweetish substance, the *nectar*, in glands or *nectaries* usually near the base of the corolla. Some insects also seek the pollen itself. The color of the petals ranges throughout almost the whole spectrum, except that green is very uncommon. The pigment may be dissolved in the cell sap, as is the case with most of the reds and blues; or may be contained in special *chromoplasts* in the petal cells, as with most orange and yellow colors.

The calyx and corolla together constitute the *perianth* of the flower.

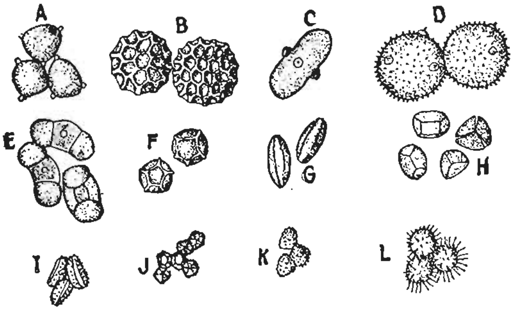


FIG. 114.—Pollen grains of various types. *A*, *Circaea; B*, *Cobaea; C*, *Morinda; D*, *Cucurbita; E*, *Pinus; F*, *Dianthus; G*, *Gentiana; H*, *Corydalis; I*, *Nymphaea; J*, *Taraxacum; K*, *Buphthalmum; L*, *Hibiscus.*

Stamens.—The next circle of floral organs, the stamens, bear little resemblance to foliage leaves, but they probably have evolved from the spore-bearing leaves or sporophylls of the lower plants. Each consists of a terminal organ, the *anther*, supported in most species by a stalk or *filament*. The anther contains (normally) two *pollen sacs* in which the *pollen grains* (Fig. 114) are produced. The pollen is liberated, when mature by the splitting open of the pollen-sac wall. Within each pollen grain are produced two male gametes, which may effect fertilization.

Pistils.—The summit of the flower is occupied by a pistil or pistils, in which the ovules or potential seeds are developed. Each unit of the pistil is believed to represent a modified seed-

bearing leaf, or *carpel*, which has become folded together so that the ovules (and later the seeds) are enclosed in a cavity or chamber. This chamber is known as the *ovary*. At its tip is the *stigma*, an organ modified to catch and hold the pollen grains. The stigma is often elevated on a stalk or *style* of considerable length.

When the pistil consists of only one carpel, as in a bean pod or pea pod, it is said to be *simple* (Fig. 116). When a single pistil represents the more or less complete fusion of two or more carpels, however, as indicated by the presence of more than one chamber in the ovary, more than one style or stigma, or by other evidence, the pistil is said to be *compound* (Fig. 117).

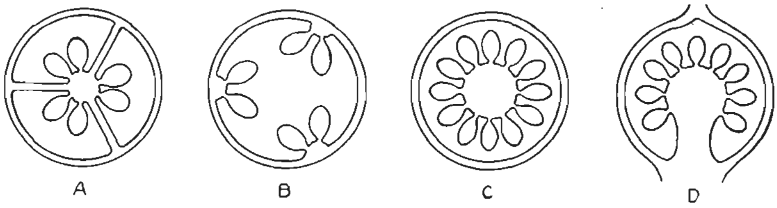


FIG. 115.—Types of placentation. *A*, axile; *B*, parietal; *C*, central; *D*, free central.

The *ovules* or potential seeds within the ovary are attached to it at definite points, lines, or areas, known as *placentae* (singular, *placenta*). The various types of placentation are shown in Fig. 115.

Imbedded in the tissue of each ovule is a single female gamete or egg cell, and surrounding the whole are two *integuments* which later develop into the seed coats. The fertilization of an egg by a male gamete from a pollen grain initiates the series of processes which result in the development of the ovule into a seed.

Variations in Floral Parts.—These four groups of organs exhibit such great differences in the number, shape, size, color, texture, and relative position of their parts as to give the flower a far greater range of external structural diversity than the other organs of the plant, and taxonomists therefore depend upon the flower very largely for those characters which distinguish genera and families of plants from one another.

In number, the floral circles may differ considerably. Among some of the more primitive orders there are several separate

pistils (Fig. 116, *A*, *B*) but, as the result of carpel fusion, this part of the flower is more often single, at least as far as its ovary is concerned. The stamens are often the most numerous of the floral parts and are generally free from one another, although

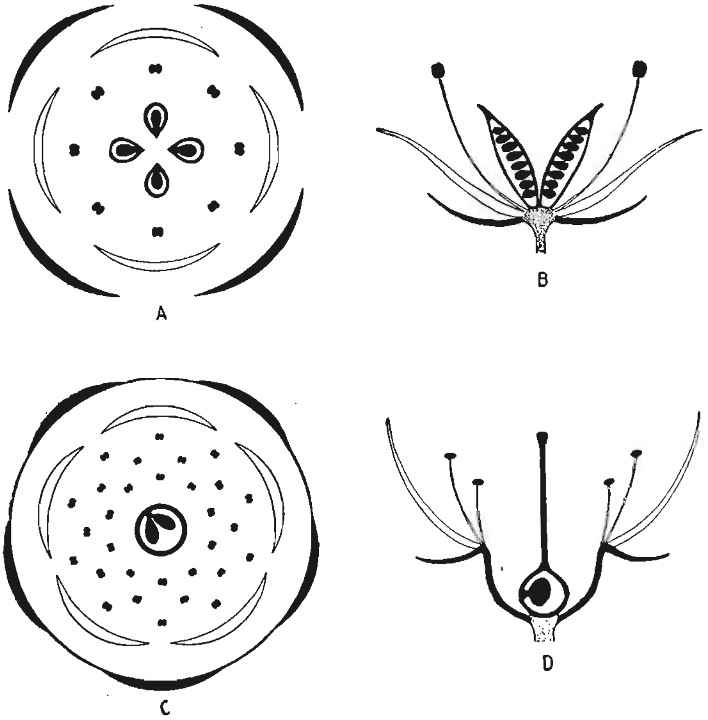


FIG. 116.—Diagrams of various types of flowers. The transverse diagrams show the numbers of parts and the relations between the members of the same circle of parts. The longitudinal diagrams show the relations between the various circles. Receptacle dotted, petals and filaments outlined, and other structures solid black. *A* and *B*, transverse and longitudinal diagrams of the flower of the stonecrop (*Sedum*). Sepals, petals, stamens and pistils are all free from one another. They are all attached directly to the receptacle, or are *hypogynous*. Each ovary is simple. *C* and *D*, cherry (*Prunus*). The sepals are united into a *gamosepalous* calyx but the petals and stamens are all separate. The corolla and the stamens are attached directly to the calyx, or are *episepalous*. The ovary has but one chamber, in which are two ovules.

in some families they may be partially fused together either by their filaments or their anthers. The petals are usually fewer than the stamens and rarely exceed ten in number. In certain orders they are united to form a continuous or *gamopetalous* (as opposed to a *polypetalous*) corolla (Fig. 117). The sepals

are generally of the same number as the petals and, like them, may sometimes be fused together into a *gamosepalous* (as opposed to a *polysepalous*) calyx (Fig. 117). Not only are the members of one circle sometimes joined together, but two entire circles may even be united. When the floral parts are attached to the

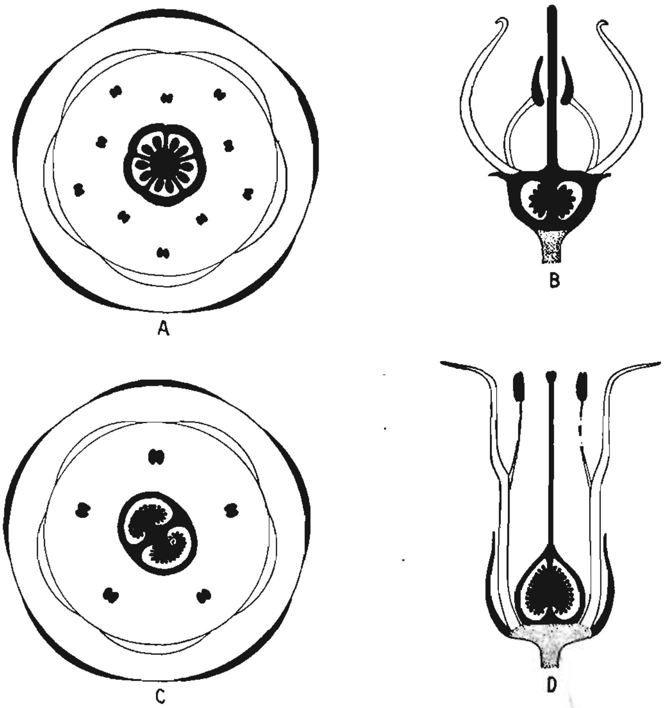


FIG. 117.—Diagrams of various types of flowers. *A* and *B*, blueberry (*Vaccinium*). The sepals are united into a gamosepalous calyx, the petals into a gamopetalous corolla, and the ovary is *compound*, with five chambers. The calyx, corolla, and stamens are united with the ovary, or are *epigynous*. *C* and *D*, tobacco (*Nicotiana*). The calyx is gamosepalous, the corolla gamopetalous, and the ovary compound, with two chambers. The calyx and corolla are hypogynous but the stamens are attached to the corolla or are *epipetalous*.

receptacle (and are thus under the ovary), they are said to be *hypogynous*. The corolla is sometimes attached to the calyx, and is thus *episepalous* or *perigynous* (Fig. 116, *D*); the stamens to the corolla (*epipetalous*, Fig. 117, *D*); the calyx to the ovary (*epigynous*, Fig. 117, *B*); and so on. In shape, floral parts vary enormously. In the higher plant groups, too, some of the sepals, petals, or stamens are different from the rest, with the result that an

unsymmetrical or *irregular* flower (Figs. 118 and 267) is produced, as opposed to the more primitive *regular* type (Figs. 113, 116, and 117). In size there is also great diversity, although flowers more than a decimeter in diameter are rare. In texture, flowers are generally soft except for the calyx, the firmness of their parts being produced by turgidity of the cells rather than by skeletal tissues. In certain cases, however, notably in the grasses and

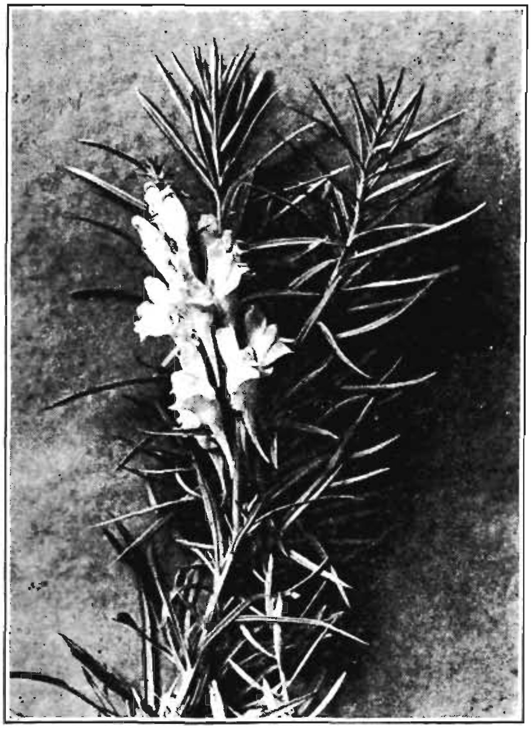


FIG. 118.—An irregular flower, the toadflax (*Linaria vulgaris*). The corolla has two lips, which are spread apart by the bee as he enters in search of the nectar, secreted by a gland or *nectary* at the end of the long spur.

allied families, the perianth segments have become hard, dry, and chaffy.

A flower with all four circles present is called *complete*, but any one, or more than one, may sometimes be absent. If both calyx and corolla are missing the flower is said to be *naked;* if the calyx is missing, *asepalous;* and if the corolla is missing, *apetalous.* If it is either the stamens or the pistil which is absent, the flower is *unisexual* or *imperfect,* and is called either *staminate* ("male") or

pistillate ("female") according to the structures which it possesses. If both staminate and pistillate flowers are distinct from one another but are on the same plant (as in corn, squash, birch, and many others) the plants are said to be *monoecious* (Fig. 119); if the two sexes are on separate plants (as in the willow, Fig. 120) the species is termed *dioecious*.

FIG. 119.—Flowers of a monoecious species, the squash (*Cucurbita Pepo*). Pistillate flower (left) and staminate one (right), with portions of corolla removed. (*From Swingle.*)

In studying the evolution of floral parts, evidence has been obtained that the earliest floral type was perfectly regular, with its various parts rather numerous and with no fusion whatever between circles or between members of the same circle. The evolutionary position of a family or other group of species within the seed plants is determined largely by the extent to which fusions and other modifications of this plan have been brought about.

Inflorescence.—The arrangement of flowers on the plant is known as the *inflorescence*. The flowers may be *solitary*, arising from the ground, or single in the axils of the leaves; or the leaves

may be reduced to small *bracts*, the internodes shortened, and the flowers thus grouped into definite clusters. Such clusters are of various types as to shape and arrangement (Fig. 121). When the first flowers to open are at the base or the outside of the cluster and are followed upward or inward by progressively younger ones, the inflorescence is said to be *indeterminate*. The most important types here are (1) the *raceme*, in which the inflorescence has a long axis and the individual flowers each are borne on a

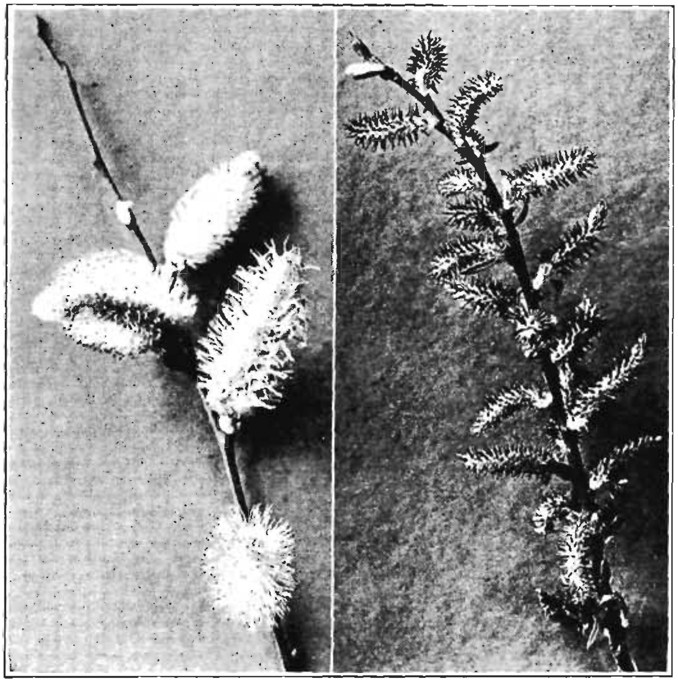


FIG. 120.—Flowers of a dioecious species, the willow (*Salix*). At left, catkins from a staminate plant; at right, from a pistillate one.

pedicel of essentially uniform length, producing a loose, elongated cluster, as in the lily-of-the-valley, the hyacinth, and many others; (2) the *spike*, similar to the raceme except that the individual flowers are borne directly on the axis, without stalks, as in the plantain; (3) the *corymb*, a flat-topped cluster where the main axis is elongated and the individual pedicels are unequal in length, as in the candytuft; (4) the *head*, where the axis is short and the individual flowers sessile, producing a roughly spherical inflorescence, as in the clover; and (5) the *umbel*, where the axis is short

but the individual flowers are on pedicels of about the same length, as in the onion; but the most familiar type is one where each primary branch of the umbel-like cluster itself bears an umbel, so that the whole inflorescence is a *compound umbel*, as in the members of the carrot family. When the first flowers to open are at the tip or inner part of the cluster, thus limiting the growth of the floral stalk, and the later ones are progressively lower or

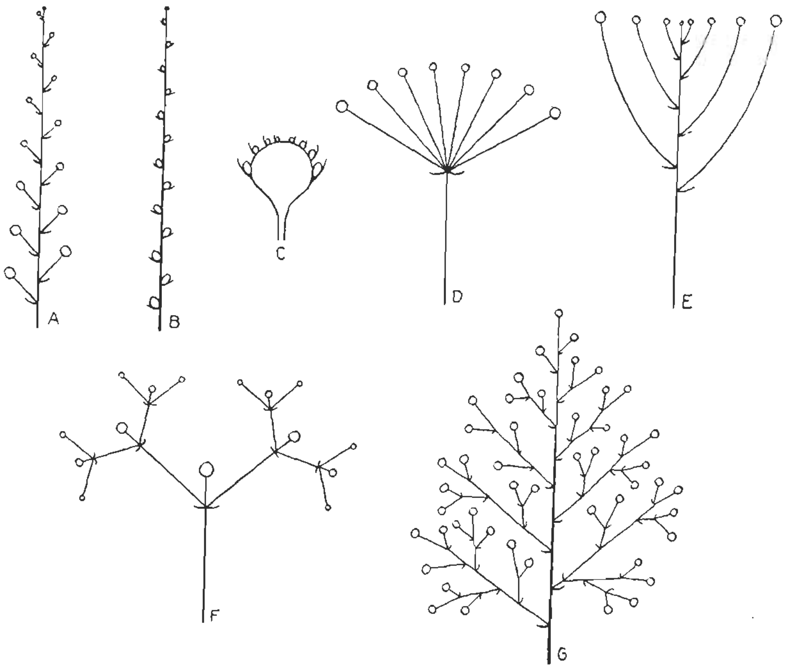


FIG. 121.– Diagram showing the arrangement of flowers in the most common types of inflorescence. *A*, raceme; *B*, spike; *C*, head; *D*, umbel; *E*, corymb; *F*, cyme; *G*, panicle.

farther out, the inflorescence is called a *determinate* one, or a *cyme*. Where the pedicels or peduncles branch, a *compound* inflorescence results, (as in the compound umbel mentioned above). A compound raceme or *panicle* is characteristic of many grasses.

Pollination.—The first step in the accomplishment of reproduction is the transfer of pollen from the anthers to the stigma, a process known as *pollination*. At about the time the flower unfolds, the anthers open and liberate the pollen grains. Sometimes the stigma lies so close to the anthers that the pollen is

transferred thereto directly, and this may happen even before the flower opens. In the great majority of cases, however, this transfer is brought about by some external agency, and pollen from the flowers of one plant is thus frequently carried to the flowers of another.

FIG. 122.—Wind-pollinated flowers of the alder (*Alnus*). The long catkins are groups of male flowers just ready to shed their pollen. The smallest catkins are composed of female flowers, their stigmas ready to receive the pollen blown through the air. The woody cones of last year, which developed from the female catkins and have shed their seed, are also shown.

The two most important agencies in effecting pollination are the wind and insects. Wind-pollinated or *anemophilous* flowers (Fig. 122) are exposed prominently on the plant but are generally small, inconspicuous, and unisexual, possessing a poorly-developed perianth, abundant dry and light pollen, and feathery stigmas. Insect-pollinated or *entomophilous* flowers (Figs. 118, 119, 260, etc.), on the other hand, are conspicuous or possess marked odor, and are characterized by a well-developed corolla, pollen grains which tend to adhere in masses, stigmas which are sticky, and in many cases by the presence of nectaries. The insect is guided to the flower by color or odor, and pollen readily adheres to its hairy body and is thus carried about from flower to flower, often coming in contact with a stigma, to the

sticky surface of which it is transferred. Insects belonging to the order Hymenoptera (the bees and their allies) are more important than any others in effecting pollination.

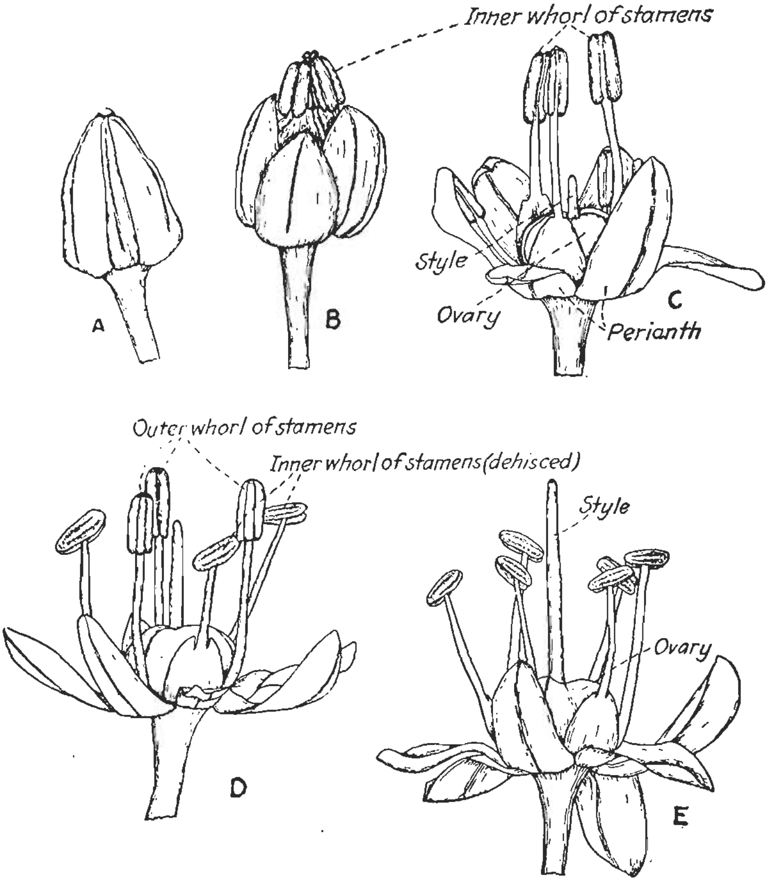


FIG. 123.—The opening of an onion flower, showing difference in time of development of stamens and stigma which prevents self-pollination. *A*, *B*, *C*, and *D*, flower unfolding and pollen being discharged. *E*, the pollen has been discharged and the stamens are beginning to wither, but the style has elongated rapidly and the stigma is now receptive. It can receive pollen only from another plant. (*From Jones and Rosa.*)

In many cases there is evidence that offspring which arise from a *cross*, or union of sexual cells contributed by two *different* parents, are superior in vigor to those in which both gametes came from the same plant. Perhaps in response to this fact, there are many devices among flowering plants which tend to

insure *cross pollination*, or the transfer of pollen from one flower or plant to another, and to prevent *self pollination*, or the transfer

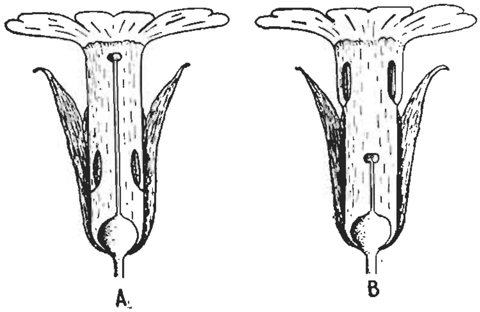


FIG. 124.—Dimorphic flowers of Chinese primrose (*Primula sinensis*). *A*, flower with long style and with stamens attached low in the tube of the corolla. *B*, flower with short style and with stamens in the throat of the corolla.

of pollen from anther to stigma of the same flower. Anthers and stigmas, for example, may ripen at different times, with the result that the anthers liberate their pollen either before the

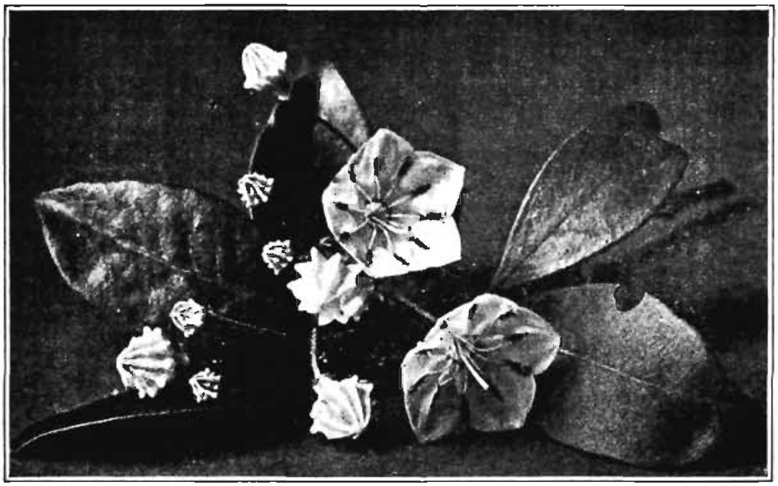


FIG. 125.—Flowers of the mountain laurel (*Kalmia latifolia*). The anthers are held in little pockets in the corolla, but the disturbance of the flower, as by the alighting of an insect upon it, will release the stamens and they will snap upward sharply, thus covering the insect with pollen.

stigma of the same flower is ripe for pollination (Fig. 123) or after it has become no longer receptive. In many cases, also, pollen from another plant is better able to effect fertilization

than the plant's own pollen; and in extreme instances the plant may actually be *self sterile*, its own pollen failing to fertilize its ovules. More striking than these methods, however, are the multitude of structural devices in entomophilous flowers whereby self pollination through insect agency is rendered difficult or impossible and cross pollination made easy. This is sometimes accomplished by *floral dimorphism* (Fig. 124), in which there are two types of flowers, so constructed that the point where the anther and stigma touch the insect's body are exactly reversed, with the result that the pollen of one is likely to reach the stigma of the other. More common are the various and often intricate devices in which hairs, springs (Fig. 125), traps, and other agencies are employed. These reach their highest development in such families of irregular-flowered plants as the legumes and orchids, and have long excited the curiosity and admiration of naturalists.

Fertilization.—Pollination, however, is only a step toward the union of male and female gametes known as *fertilization* (Fig. 126). Although the pollen grain is a single cell, it is not the male gamete. At about the time of pollination, the nucleus of the grain divides into two, one of which, the *tube nucleus*, remains free in the cytoplasm. The other nucleus surrounds itself with a mass of cytoplasm of its own, sometimes with a separate wall, and is known as the *generative cell.* Shortly after the pollen has reached the stigma it germinates through contact with the stigmatic fluid. The thick wall of the pollen grain bursts at one point and out of the grain proceeds a thin-walled *pollen tube.* Near the tip of this moves the tube nucleus, followed by the generative cell (Fig. 127). This tube grows down through the tissues of the style (which in some cases is hollow or partly so), and carries the contents of the pollen grain into the ovary and to the mouth of the ovule (Fig. 126, *C*). Meanwhile the generative cell divides into two *male cells*, which are the true male gametes.*

By this time the ovule has become prepared for fertilization. It possesses one or two coats or *integuments*, later developing

* One of the cell divisions just preceding the formation of both the male and the female gametes is a *reduction division*, whereby the number of chromosomes is halved. Each gamete thus contains half the number of chromosomes found in an ordinary body cell. The double number is restored in the fertilized egg through the union of the two gametes. (See page 388).

into the seed coats, which cover it except at one point, the mouth or *micropyle*. Here the pollen tube usually enters. Inside the integuments is a thin nutritive layer, the *nucellus*. Within this, in turn, and ordinarily occupying the whole central portion of

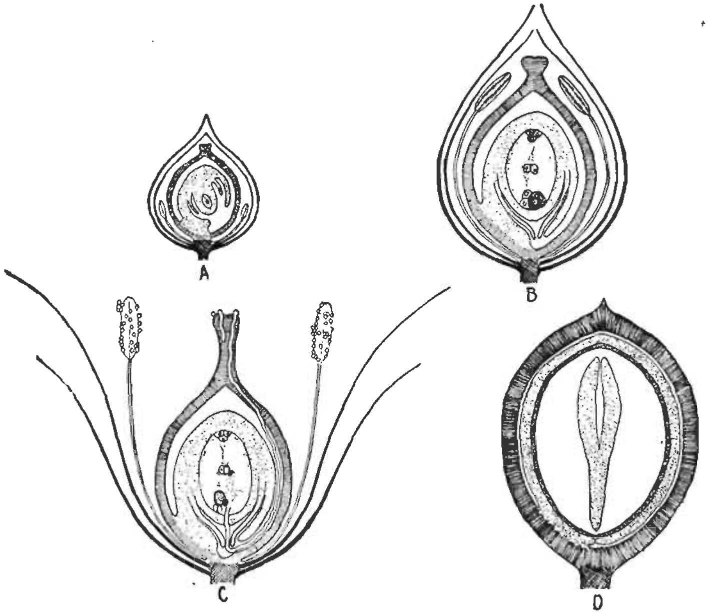


FIG. 126.—*The process of seed-production in a flowering plant.* Longitudinal diagrams of flower and fruit, the calyx and corolla solid black; the ovule, seed-coats and embryo dotted, and the ovary wall, style, and stigma lined. *A*, young bud, the stamens and the single ovule beginning to develop. *B*, bud ready to unfold. The embryo sac within the ovule is fully developed and the egg (below) and double endosperm nucleus (in center) are ready for fertilization. *C*, fully opened flower. The anthers have burst and pollination has taken place, pollen grains being transferred to the stigma. Two grains have germinated, and the pollen tube from one of them has penetrated the style, entered the ovary, passed through the micropyle of the ovule and discharged its contents—the two male gametes—into the embryo sac. Double fertilization is taking place, one male gamete uniting with the egg and the other with the endosperm nucleus. *D*, ripe fruit. Sepals, petals, and stamens have dropped off; the ovary wall has hardened into the pericarp; the micropyle has closed; the integuments have become seed coats and the ovule has developed into the seed. The embryo, in the center of the seed, has grown from the fertilized egg, and the endosperm surrounding it (shown in white) from the endosperm nucleus.

the ovule, is the *embryo sac*. This is a small, sap-filled cavity with three cells at each end and a naked nucleus, the *endosperm nucleus*, near its center. The three cells at the end of the sac farthest from the micropyle play no part in fertilization or seed development. Of the three at the micropylar end, however, one

is usually distinguishable by its greater size, and constitutes the female gamete or *egg*. *With the nucleus of this egg cell fuses one of the male gametes which has come down the pollen tube* (Fig. 126, *C*). This union produces the *fertilized egg*, and *from this single cell* develops the entire embryo of the seed and thus the young plant which grows therefrom. This fertilized egg, in which are combined the protoplasm of the two parents, is the *sole* direct, living link between parents and offspring; and only across this exceedingly narrow bridge are characteristics transmitted by inheritance from one generation to the next.

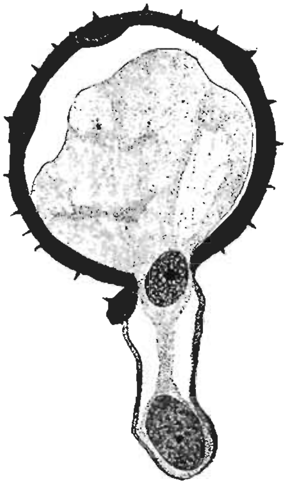


FIG. 127.—Germinating pollen of squash. The pollen grain has burst and a pollen tube is starting down through the style. Near the end of the tube is the tube nucleus. Some distance behind is the generative cell, from which are later developed the two male cells. (*From A. I. Weinstein.*)

The fertilization of the egg by a male cell is not the only cell union which takes place at this time, for the other male cell fuses with the endosperm nucleus (Fig. 126, *C*), and from the cell thus formed arises the *endosperm* or food-storage tissue of the seed.

Fertilization effected by gametes from the same plant is known as *self fertilization;* that by gametes from different plants as *cross fertilization.*

Seed Development.—After fertilization has been effected, the petals and stamens drop off and the ovule gradually develops into the *seed* (Fig. 126, *D*). Various changes accompany this process. The whole structure grows markedly in size and the

integuments increase in thickness, become hard and woody, and close over the micropyle, which appears as a minute opening in the seed coat or may even be obliterated. The scar or *hilum* is the point at which the seed broke away from the stalk, or *funiculus*, whereby it was attached to the placenta. In many seeds a considerable mass of *endosperm* or food-storage tissue is developed, but in others this is much less abundant.

Within the endosperm is the *embryo* or young plant itself, which has developed from the fertilized egg. In dicotyledonous plants (p. 413) the embryo is differentiated into three main portions; the *hypocotyl* or primitive stem and root, its tip directed

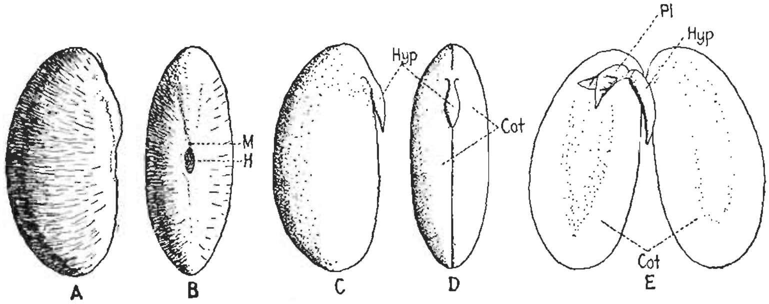


FIG. 128.—The structure of a seed. *A* and *B*, side and face views of a bean seed. *C* and *D*, side and face views of the embryo after the seed coats have been removed. *E*, the two cotyledons spread apart, revealing the plumule within. *M*, micropyle; *H*, hilum; *Cot.*, cotyledons; *Hyp.*, hypocotyl; *Pl.*, plumule.

toward the micropyle; the two seed leaves or *cotyledons*, attached to the upper end of the hypocotyl, and the *plumule* or bud, inserted between the cotyledons (Fig. 128). In such seeds as those of the bean, all the stored food is in the tissues of the embryo itself, particularly the cotyledons, and these consequently are very thick and have almost entirely lost their leaf-like appearance. In the pea they even may remain underground when the seedling grows. In such seeds the plumule is large and soon starts vigorous growth into a foliage-bearing shoot. Other plants, of which the castor bean, morning-glory, and buckwheat are commonly-cited examples, bear seeds in which most of the reserve food is stored in the endosperm. As a result, the cotyledons are relatively broad, thin, and leaf-like, and may function as foliage leaves for some time, the plumule here being small and slow to develop. In seeds of the squash and many other plants, the cotyledons are intermediate in type between these two.

Among *monocotyledonous* plants (p. 413) endosperm is always well developed and the comparatively small embryo consists of a flat disc, the *scutellum* (which probably represents a single cotyledon), to the face of which are attached an upward-pointing, sheathed *plumule* or bud and a downward-pointing miniature root or *radicle* (Fig. 129). The scutellum serves to absorb food from the endosperm and to transmit it to the growing portions of the embryo.

The ripe seed is thus a structure in which the partially developed young plant, well protected and provided with an abundant supply of food for future growth, is able to pass through a more or less extended period of dormancy.

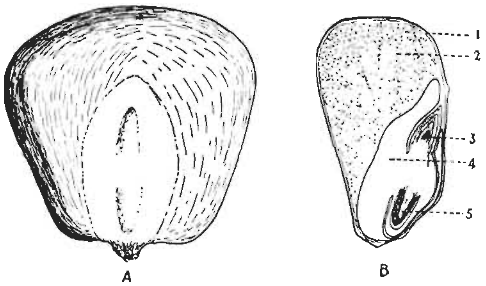


FIG. 129.—A kernel (grain or fruit) of corn. *A*, face view, showing outline of embryo in the middle; *B*, longitudinal section. 1, pericarp and seed coat, fused. 2, endosperm. 3, plumule. 4, scutellum (cotyledon). 5, radicle. 3, 4, and 5 constitute the embryo.

The Fruit.—The ripened ovary, together with its contents, the seeds, and with any other structures intimately associated with these, is known as the *fruit*. The development of the ovary into the fruit involves other changes than the growth of ovules into seeds, chief among which is the ripening of the ovary wall into a *pericarp*. These changes result from the stimulus produced by fertilization, and (except in rare cases of *parthenocarpy*) will not take place otherwise.

Fruits are various, and many different types are recognized and named. In one group the pericarp when ripe is dry, and in the other it is fleshy. The most important of the various fruit types under each of these groups may be distinguished briefly as follows:

Dry Fruits. *a. Pod or Legume.*—Fruit splitting open when ripe and developed from a single carpel or simple ovary, as in the pea and bean.

b. Capsule.—Fruit splitting open when ripe but developed from a compound ovary, as in the lily.

c. Achene.—Fruit not splitting when ripe, single seeded, with the seed attached to the pericarp at only one point, as in the sunflower, buttercup, and buckwheat.

d. Caryopsis, or Grain.—Like the achene except that the coat of the single seed is fused tightly to the pericarp. This is the characteristic fruit of the grass family, which includes all the common grains.

e. Nut.—A one-seeded fruit with a very woody pericarp, as in the walnut.

Fleshy Fruits. *f. Berry.*—The entire pericarp fleshy and surrounding one or more seeds, as in the grape, currant, and tomato. Modified types of berries are the *pepo*, characteristic of the squash and melon families, in which there is a hard shell outside the fleshy portion; and the *hesperidium,* characteristic of the citrus fruits, where the rind is leathery.

g. Drupe, or Stone Fruit.—A one-seeded fruit with its pericarp differentiated into an outer fleshy *exocarp* and an inner, stony *endocarp,* as in the cherry, peach, and olive.

h. Pome.—The fleshy portion of the fruit consisting of the enlarged and ripened receptacle which surrounds the ovary, the latter forming mainly the papery "core," as in the apple.

Seed Dispersal.—It is obvious that to leave successful offspring a plant must not only develop seeds but must provide for their dispersal; and in bringing this about, almost as great a variety of adaptive devices are employed as there are to insure cross pollination. Dependence is placed upon various agencies, but chiefly the wind and animals. Many seeds or even entire fruits are light and provided with wings or tufts of long hairs, so that they present a large surface for the wind to catch, and are often wafted many miles (Fig. 130). In the case of the various "tumble weeds," the entire plant breaks off at the base of the stem and is rolled along over the ground by the wind. Other fruits and seeds develop hooks (Fig. 131), spines, or sticky secretions which enable them to adhere to the fur of animals or the feet of birds and thus to be carried for long distances. In fleshy fruits, the fleshy portion or pulp is usually bright in color (Fig. 131), and is rendered attractive to animals by its taste. Birds are particularly important in the dissemination of the seeds of such fruits. In a few cases like the witch hazel, the fruit splits open with such force that the seeds are projected through the

A B

FIG. 130.—Seed dispersal by the wind. *A*, ripe fruit of the milkweed (*Asclepias*). Each seed is provided with a tuft of feathery hairs, which aid in the dispersal of the seeds by the wind. *B*, fruits of the cotton-grass (*Eriophorum*). Each tuft in the picture is composed of a group of single-seeded fruits, attached to each of which is a cluster of long, cottony hairs.

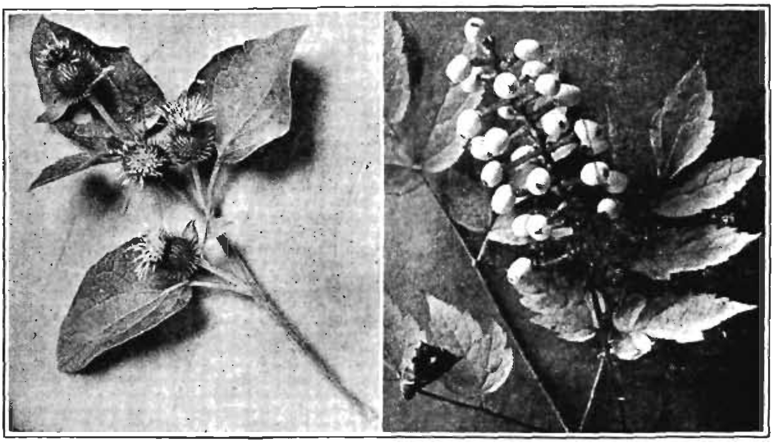


FIG. 131.—Seed dispersal by animals. At left, flower and fruit clusters of the burdock (*Arctium*); the bracts which surround the cluster are stout and hooked, and thus aid in the dispersal of the fruit. At right, conspicuous berries of the baneberry (*Actaea*).

air for a considerable distance. The seeds and fruits of water and shore plants are usually dispersed by floating on the water and have been known to travel thus for hundreds of miles.

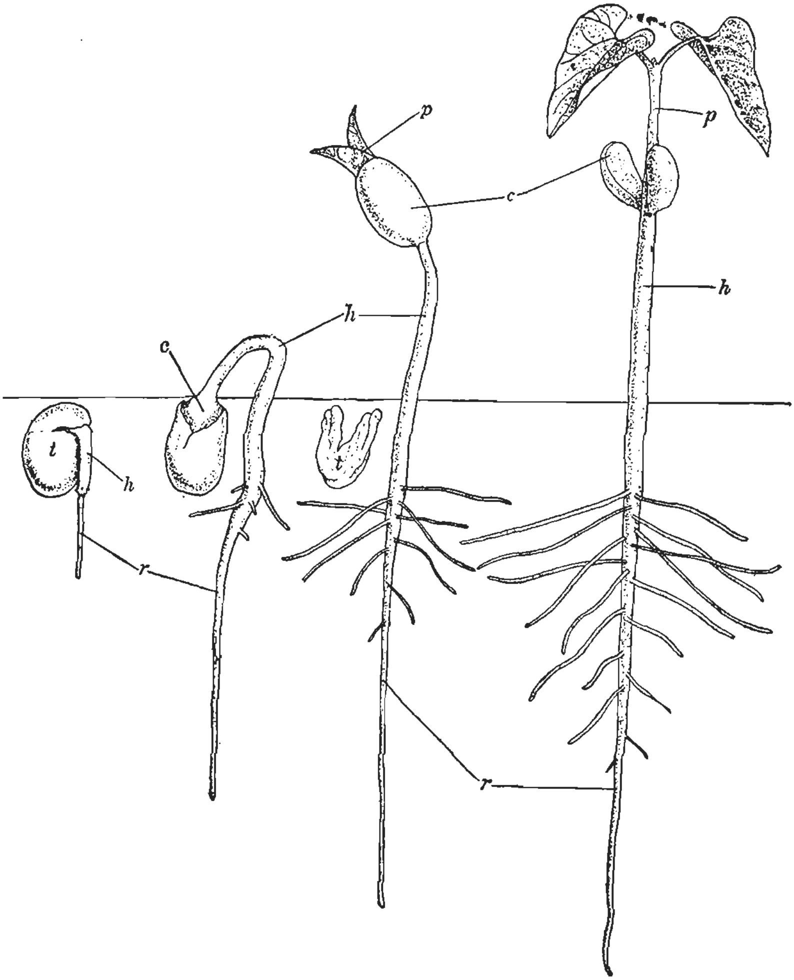


FIG. 132.—Germination of the seed Successive stages in the development of the bean seedling. *t*, seed coat; *h*, hypocotyl; *r*, primary root; *c*, cotyledons; *p*, plumule and the shoot into which it develops. (*From Haupt.*)

Seed Germination.—The seed remains dormant until favorable conditions appear, when it begins to sprout or *germinate* (Fig. 132). These conditions are a moderately high temperature, a plentiful supply of water and oxygen accessible to the embryo,

and a sufficient degree of ripeness in the embryo itself. Hard seed coats may greatly delay germination by their mechanical strength or by their impermeability to water or oxygen or both. In such cases the coat must decay, or must be broken artificially before the seed will sprout. Some seeds, even when external conditions are favorable, will remain dormant until a gradual process of ripening is accomplished. This may sometimes be hastened artificially by low temperatures and by the influence of chemical substances.

When favorable conditions appear, metabolism begins vigorously in the embryo and in the cells of the endosperm. Water is absorbed in large quantities and the embryo swells, bursts the seed coats, sends its root into the ground and its stem into the air, and becomes a *seedling.* The food stored in endosperm or cotyledons is digested and used for the development of new organs. It is generally sufficient in amount to provide for the growth of the seedling to a point where the latter can begin to manufacture its own food.

In species where the cotyledons are very stout and packed with food, they sometimes remain under ground in germination, as in the pea, and only the plumule appears above the surface. In other cases, where the cotyledons are somewhat less thick, they are elevated above the ground by the elongation of the hypocotyl, as in the bean, and may turn somewhat green; but they ultimately shrivel and drop off. In seeds with thin cotyledons, these are exposed immediately to the light and serve as foliage. In monocotyledonous seeds, the single cotyledon functions chiefly in absorbing food from the endosperm.

The first stages in germination are made at the expense of food stored in endosperm or cotyledons but, through the growth of the plumule, typical foliage leaves are developed which assure an independent food supply. The young plant soon outgrows the seedling stage and reaches maturity, at which point the cycle of reproduction is complete.

QUESTIONS FOR THOUGHT AND DISCUSSION

470. Is asexual reproduction commoner among animals or among plants? Explain.

471. Give an example (other than those mentioned in the text) of a plant which commonly reproduces itself asexually.

472. What advantage is it to the potato plant to reproduce itself by tubers rather than by seeds? What disadvantage is there in this process?

473. What relation can you suggest between the stationary habit so characteristic of plants and their reproduction by means of flowers?

474. What advantages and disadvantages have monoecious and perfect-flowered plants as compared with dioccious ones?

475. The petals of a flower usually drop off after fertilization occurs but the sepals commonly remain. Of what advantage is this fact to the plant?

476. Pollen grains, particularly in wind-pollinated flowers, tend to have a much-roughened surface. What advantage may this confer?

477. Asthma and "hay fever" have been found to be due in many cases to the inhalation of pollen. What types of plants are probably chiefly concerned in causing these ailments?

478. What suggestions can you make as to why a pollen grain germinates on the stigma and as to why the pollen tube grows down the style directly to the ovule?

479. Why is pollen generally spoiled if it is wet by rain?

480. What effect does the weather at apple-blossom time have upon the size of the subsequent apple crop?

481. Do you think that the earliest seed plants were pollinated by wind or by insects? Explain.

482. What advantages and what disadvantages are there in wind pollination?

483. Why do trees which are wind-pollinated usually flower early in the spring?

484. The flowers of most coniferous trees are borne near the ends of the branches, and the flowers of grasses are usually raised up on a tall spike. Explain these facts.

485. What advantages and what disadvantages are there in insect-pollination?

486. Why are the corollas of most flowers some other color than green?

487. Why are low-growing plants almost always pollinated by insects?

488. Why are alpine flowers usually brilliant in color or otherwise conspicuous?

489. Why are night-blooming flowers usually white?

490. Why are low-growing and inconspicuous flowers often very fragrant?

491. In many plants the flowers are arranged in clusters. Of what advantage is this to the plant?

492. In most flower clusters, the flowers open a few at a time rather than all at once. Explain.

493. Are solitary flowers usually larger or smaller than those which occur in clusters? Explain.

494. Do you think that bees are attracted to flowers by the same odors which are attractive to human beings? Do you think that the same holds true for flies? Explain.

495. Most flowers do not exceed a decimeter in diameter and the great majority are very much smaller. What do you think it is that determines this general flower size?

496. Many flowers are so constructed as to admit bees readily but to exclude ants. Explain.

497. It is a general rule that plants with flowers rich in nectar tend to have hairy stems and flower stalks. Explain.

498. In many plants, the removal of the stamens as soon as the bud opens causes the flower to remain in bloom longer than it would if the stamens were left attached. Explain.

499. What means of dispersal have plants aside from the dispersal of their seeds? Cite examples.

500. Other things being equal, which type of plant will become dispersed more rapidly, a tree or an herb? Explain.

501. What advantage is it to a berry-bearing plant to have its fruits brightly colored?

502. What color prevails in unripe fruit? Explain.

503. Why is green such an uncommon color among ripe fleshy fruits?

504. In the case of fleshy-fruited plants, of what use to the plant are the sugars and other foods which occur in the fleshy portion of the fruit?

505. The flower stalks of the dandelion elongate after the seeds are ripe. Explain.

506. As a general rule, how tall are plants in which the fruit bears hooks or similar structures? Explain.

507. Just what part of the seed develops into a new plant?

508. Why does cracking or chipping the shell of a hard-shelled fruit or seed often hasten its germination when planted?

REFERENCE PROBLEMS

124. When and by whom was sexuality in plants discovered?

125. What relationship has there been between the evolutionary history of insects and of flowering plants?

126. What plant species are there which depend upon flies rather than bees for pollination? How do their flowers differ from those of ordinary plants?

127. Does a bee visit all plant species, one after the other, on the same trip, or does he confine himself to one? Of what importance to plants is this behavior?

128. Some varieties of strawberries will set seed when planted by themselves, but others will not. Explain this difference.

129. One corn stalk alone in a field will usually produce few or no seeds. Cucumbers and melons will not fruit naturally in greenhouses, at least in the winter. Explain these facts.

130. Draw up a list of at least ten plant species which are monoecious and ten which are dioecious.

131. What is the phenomenon of *xenia?* Of what economic importance is it?

132. Describe the peculiarities of reproduction shown by the fig.

133. Give examples (other than those mentioned in the text) of a capsule, a pod, an achene, a nut, a grain, a berry, a drupe, and a pome.

134. What different constituents of the wheat kernel are found in ordinary white flour; in whole-wheat flour; in gluten flour?

135. Name three cultivated fruits which are essentially seedless.

136. Give the author and title of three important books dealing with plant reproduction or some of its phases (exclusive of inheritance), and outline briefly the content of each.

137. Name several botanical investigators who have done important work on plant reproduction, and state the notable contributions made by each.

138. Give the derivation of the following terms and explain in what way each is appropriate:

Calyx	Petal	Hypocotyl
Corolla	Stamen	Micropyle
Perianth	Pistil	Cotyledon
Sepal	Ovule	Plumule

CHAPTER XI

HEREDITY AND VARIATION

As a result of the process of reproduction described in the preceding chapter, a continuous succession of new individuals arises. One of the most remarkable features of this reproductive activity is that each of these new individuals bears a very close resemblance to its parents. The offspring of wheat plants are always wheat plants and nothing else; and the offspring of oak trees are always oaks. Furthermore, any particular kind or variety of wheat or of oak will produce (under proper conditions) plants of that kind or variety. This tendency for offspring to display the particular characteristics which distinguish their parents is termed *heredity*.

Heredity.—Attention already has been called to the exceedingly narrow physical bridge—the reproductive cells or *gametes*—which connects one generation with the next. To its offspring, one parent plant contributes a single male cell and the other parent a single egg cell, and out of the fertilized egg arising from the fusion of these two gametes the new individual develops (Fig. 133). It is evident, therefore, that the parental characteristics must be transmitted in some way in the protoplasm of these tiny sexual cells. Any actual plant character (such as redness of flower or tallness of stem) obviously cannot be found in these cells; but something representing it, and capable of producing it in the new plant, must be there. This "something" —its real nature is still obscure—is called the *factor* or *gene* for the character in question. In a wheat plant, for example, the height and strength of the stem, the shape and texture of the leaf, the number of spikelets in the head, the shape, color, and surface of the glumes, the weight of the kernel, the character of the grain, the yield of seed, the resistance of the plant to cold, drought, and disease, together with a host of other characteristics, have all been shown clearly to be inheritable. It is evident that in every male gamete and in every female gamete there must be a factor or factors which represent each of these

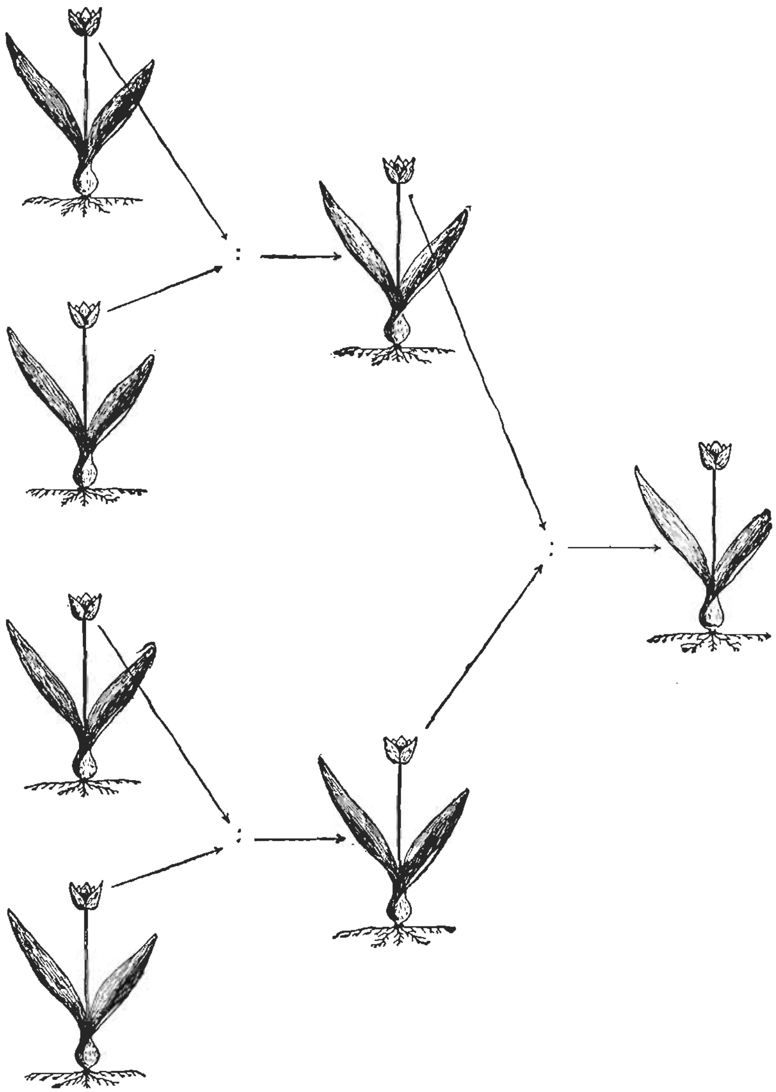


FIG. 133.—The narrow hereditary bridge. The plant at the right receives from each of its parents only one minute sexual cell, a male gamete from one and a female gamete from the other. The parents, in turn, receive from each of the grandparents but one sexual cell. Thus the bridge which connects one generation with the next, and over which the entire inheritance must pass, is an exceedingly narrow one. The real gametes are very much smaller, both actually and in proportion to the size of the plant, than the dots by which they are here represented.

characteristics and which thus determine the particular kind of wheat plant which is to be produced. These minute particles of protoplasm, into which so much is packed and out of which so much emerges, are certainly among the most remarkable bits of matter in existence.

Variation.—Close as the resemblance is between parent and offspring, however, it is almost never an exact resemblance. Any individual plant or animal, if studied carefully enough, will

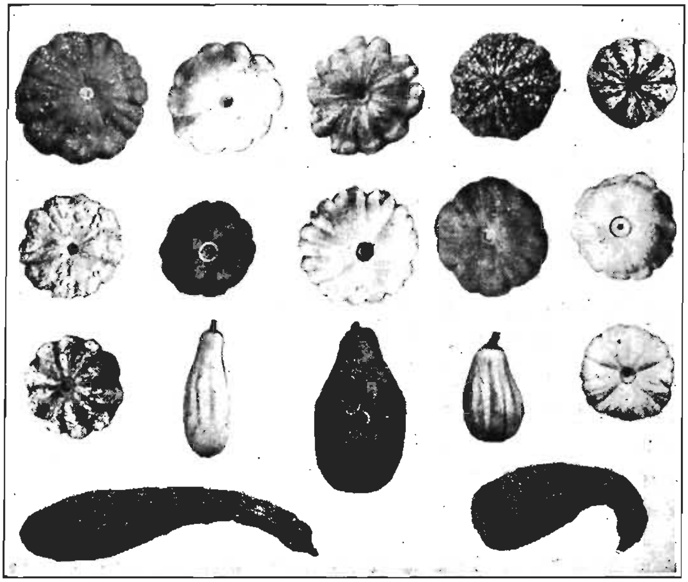
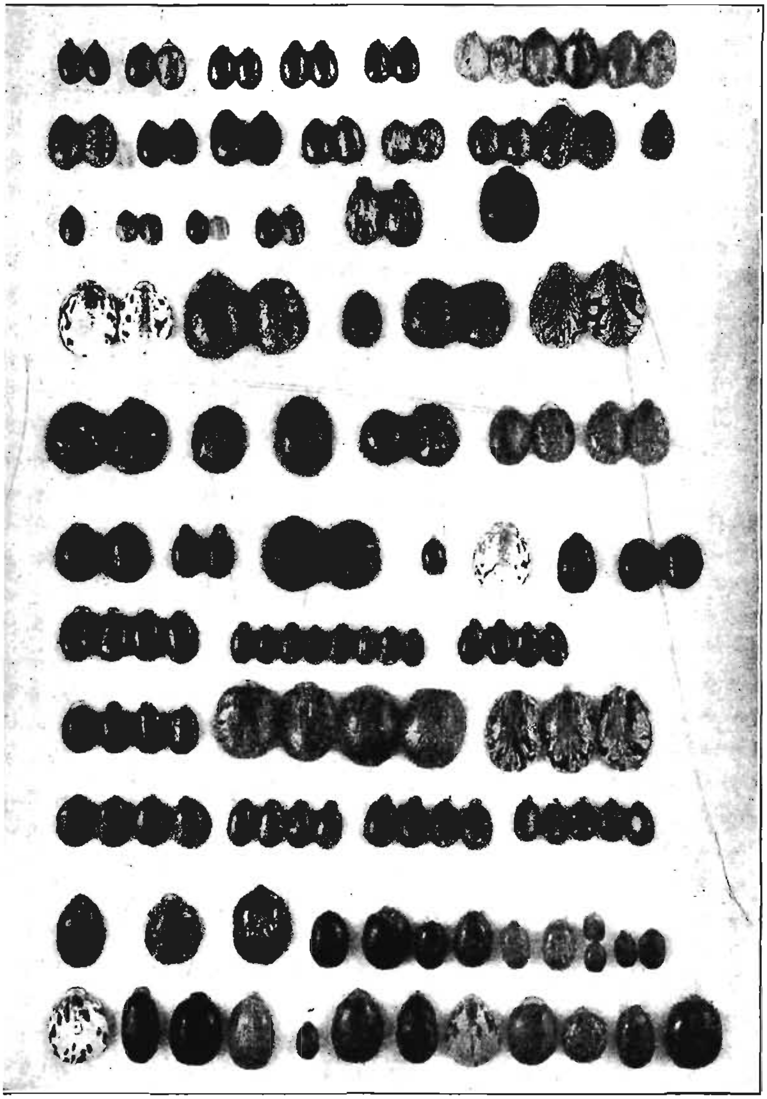


FIG. 134.– Variation in color, shape, size, and surface in the fruit of the summer squash. All of these types may appear among the descendants of a single individual.

be found to differ somewhat, even though very slightly, both from its parents and from its fellow offspring. These differences are known as *variations* (Figs. 134 and 135), and their presence brings about that variability which is so characteristic of all living things.

Laws of Inheritance.—The close attention given to the problems of breeding by those who have been responsible for the steady improvement of domesticated animals and plants through the centuries has been rich in practical gains, but it has contributed little to an understanding of inheritance beyond a recognition of these two main facts of heredity and variation. Man



'IG. 135.—Variation in shape, size, color, and pattern in the seeds of the castor bean (*Ricinus*). (*From White.*)

long has known that "like begets like" and that offspring differ among themselves; and he has used this knowledge in choosing the best individuals and breeding from them. In this way breeders have made steady improvement, but this improvement has been due largely to sharpsightedness in seizing upon favorable variations rather than to a fundamental understanding of inheritance which would enable the breeder to control the process and predict its results. Within the past century, however, and particularly within the past thirty years, notable advances have been made in this field of knowledge, and biologists have found that there are indeed *laws of inheritance*, an understanding of which will raise the art of breeding from clever but uncertain guesswork to such a firm scientific basis as that upon which chemistry and physics now rest. An investigation of these laws is the province of the modern science of *genetics*.

Inheritance of Acquired Characters.—It has been learned, for example, that all variations do not behave alike in inheritance. Some are due to factors embodied in the constitution of the gametes and may thus be transmitted from one generation to the next. They are clearly inheritable and are the "raw material" with which the breeder may work. Other variations, and among them many important ones, result from the direct action of the environment upon the plant body during its growth, and apparently are never transmitted to offspring. Such "acquired" characters are the increased size and vigor which result from growth in rich soil (Fig. 136), the thick leaves developed by many plants when exposed to bright sunlight, the galls and other malformations resulting from insect or fungus attack, the stunting effect of overcrowding (Fig. 137), and many others. These variations merely affect the individual and do not reappear in the offspring unless the particular environment which has caused them persists. Acquired variations of this kind are of particular interest to the farmer or to anyone who is concerned with plant culture, since they can be controlled readily by a proper manipulation of the environment; but the breeder and the student of inheritance must learn to recognize them and to realize that they are quite valueless for his purposes. Good care and cultivation will bring out the best that there is in a poor race of plants but can never change a poor race into a good one.

Mendel's Laws of Inheritance.—It is therefore only with those characters which are clearly inherited that the student of genetics

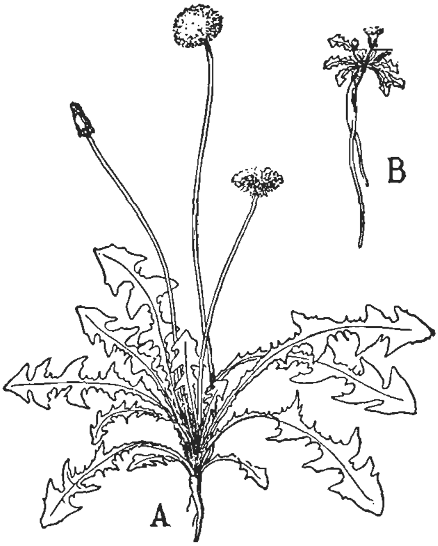


FIG. 136.—Variation produced by the environment. *A*, plant of dandelion (*Taraxacum*) grown in a lowland garden; *B*, portion of the same plant grown in an alpine garden, under relatively unfavorable conditions. (*From Bonnier.*)

FIG. 137.—Variation due to crowding. Well-spaced corn plants at left; crowded ones of the same variety at right. (*From Blakeslee.*)

is concerned. As he studies their behavior in the passage from generation to generation he notices many apparent irregularities. The same parents will transmit different characters to their different offspring. Sometimes a particular parental character will fail to appear in the offspring at all. In other cases the offspring will develop characters possessed by neither of its parents but sometimes found in a more remote ancestor. It is these facts which genetics is endeavoring to explain and to reduce to definite laws. The most notable of these laws, and

FIG. 138.—Gregor Johann Mendel, 1822–1884. (*From Genetics, by permission.*)

the ones which constitute the basis of modern understanding of inheritance, were formulated by Gregor Mendel (Fig. 138), an Austrian monk, over sixty years ago. He published the results of his experiments in 1866, but they were ignored at the time, and their great importance was not recognized until 1900. Since that date many investigators have studied diligently the applications of "Mendelism" in the inheritance of a wide variety of animals and plants, and although advancing knowledge has resulted in many amplifications and interpretations of these laws, they still remain fundamentally intact as the cornerstone of the science of genetics.

In his cloister garden Mendel studied inheritance in peas, making hybrids between different types and studying the results from generation to generation. His method of attack on the problem differed in several important respects from that of previous workers. First, in his crosses between contrasting types Mendel singled out a particular character of the plant and followed out its behavior by itself, instead of trying to study the whole complex individual at once. In this way the inheritance of flower color, of seed color, of seed surface, of plant height, and of several other characteristics of the garden pea were investigated. Second, he kept accurate pedigree records, making sure that he knew the exact ancestry of every individual plant and the characters displayed by each of its ancestors and descendents. This method involves much care and pains, both in making artificially the particular pollinations desired and in preventing all pollinations by such uncontrolled agencies as insects and the wind; and the labor of keeping the records is often very great. Mendel's method is now almost universally adopted, however, by students of inheritance. Third, in each generation where contrasting characters appeared (both purple flowers and white ones in the offspring from a single cross, for example) he carefully *counted* the number of individuals of each type and thus obtained a mathematical statement of the facts. In short, Mendel applied the true *experimental* method to the problems of heredity.

The results derived by this novel and painstaking method of investigation were reported carefully by Mendel, and his interpretations thereof have come to be known as Mendel's Laws. These are a series of distinct principles, the important points of which will now be discussed briefly.

Unity in Factors and Characters.—As a general result of his hybridization experiments, Mendel observed that the plant seems to behave in inheritance as though it were an aggregation of independent and separable characteristics, each of which is perfectly distinct and may exist with any combination of other characters in a given individual. These traits he called "unit characters." It is now recognized that the expression or appearance of these characters may vary considerably under different conditions and that the real unity lies rather in the underlying factor than in the visible (and perhaps variable) character which it produces. The essential point, however, is that the organism, so far as its behavior in inheritance is concerned, seems to be

made up of distinct and independent units. Purple flower color in peas, for example, is such a unit, and may be associated with either yellow or green seed color, wrinkled or smooth seed surface, tallness or dwarfness of vine, and so on. A skilful breeder thus may combine and rearrange the characteristics of his plants almost at will.

Dominance.—Mendel's studies also brought out the fact that when plants which are dissimilar in a given feature (such as

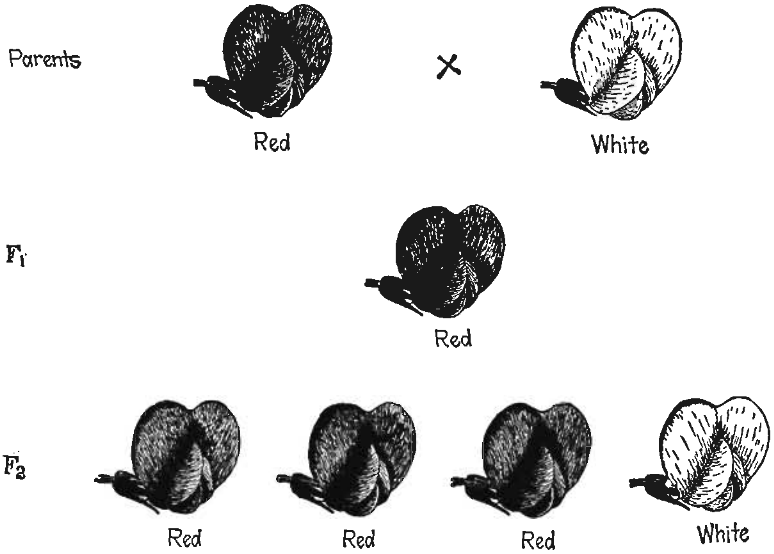


Fig. 139.—Cross between a pure colored-flowered and a white-flowered pea plant, showing the dominance of color in the F_1. If an F_1 plant is self fertilized the resulting F_2 generation is three-fourths colored-flowered and one-fourth white-flowered.

flower color, for instance) are crossed, the two characters thus brought together differ markedly in ability to express themselves in the resulting hybrid plant. When a pure purple-flowered plant is crossed with a pure white-flowered one, for example, *all* the offspring resemble the purple parent in their flower color. Such a character as purple flower color in peas Mendel therefore termed *dominant* and one like white flower color, which fails to appear in such hybrid offspring, he called *recessive* (Fig. 139). A pair of contrasting characters like these are known as *allelomorphs*. All the characters studied by Mendel happened to show complete or almost complete dominance or recessiveness, but many instances

have since been found where a hybrid plant resembles neither parent exactly with respect to a given character-pair but is more or less intermediate between them (Fig. 140). Such cases of the incomplete or imperfect dominance of one character over another in the hybrid state are much more common than those in which dominance is complete. The essential fact to be emphasized, however, and one that is of great practical import, is that the *appearance* of a plant (or animal) does not necessarily indicate its

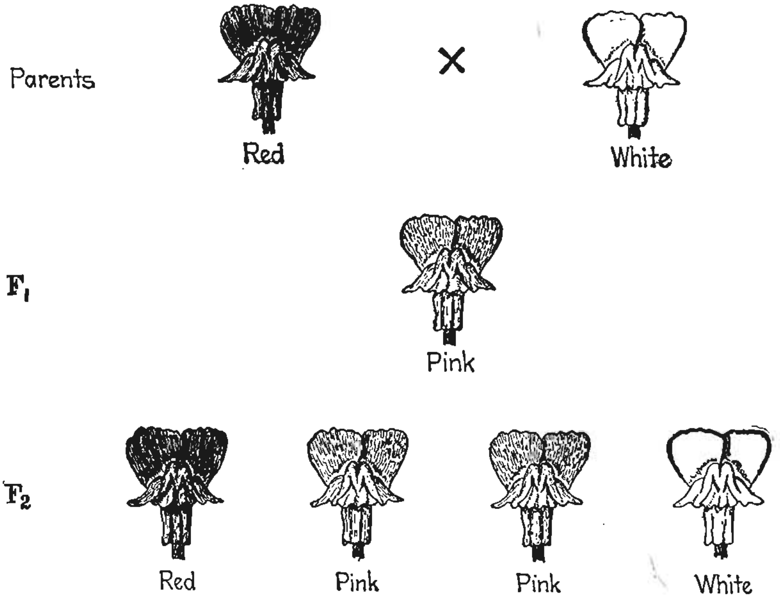


Fig. 140.—Cross between a red-flowered and a white-flowered snapdragon, showing absence of dominance in F_1. If an F_1 plant is self-fertilized the resulting F_2 generation is one-fourth red, one-half pink, and one-fourth white.

ancestry or its genetic make-up. Dominance, partial or complete, may enable a hybrid or mongrel to masquerade as a pure or superior individual.

Segregation.—Of much more importance than this fact of dominance in the hybrid was Mendel's discovery of the manner in which characters are transmitted to the second and later generations following a cross. The hybrid offspring arising from a cross between a plant of a purple-flowered race and one of a white-flowered race are, as has been said, all purple. In appearance they resemble rather closely the purple-flowered

parents, but in most such crosses the hybrids are often somewhat paler than the pure colored types. When two of these *hybrid* colored plants are crossed, or when one of them is self fertilized (which amounts to the same thing genetically) both purple-flowered and white-flowered plants appear in their offspring, the former constituting about three-fourths and the latter about one-fourth of the total number of individuals in the progeny (Fig. 139). These white-flowered plants *breed perfectly true* when self fertilized, and purple color never appears in subsequent generations of their descendants when inbred. A part of the colored plants (approximately one-third of them) breed perfectly true to the purple color, none of their offspring, when inbred, possessing white flowers. The rest of the colored-flowered plants, however, (about two-thirds of them, and thus about one-half of the total number of the offspring) resemble the hybrids in color and behave when self-fertilized exactly as did the hybrids, producing offspring of which three-fourths are colored and one-fourth white. These facts are set forth diagrammatically, for a case where dominance is absent, in Fig. 141.* This separation and sorting out of characters which occurs in offspring of hybrid plants is known as *segregation*. The discovery and interpretation of segregation were perhaps the most important contributions which Mendel made to our knowledge of inheritance.

The essential character of segregation is shown in the behavior of contrasting factors when they exist together in a hybrid individual. A factor transmitted through the gametes of one parent and a contrasting factor transmitted through the gametes of the other parent, come together and co-exist in the cells of the hybrid offspring plant *without blending or losing their identity;* and when such a hybrid plant produces its own sexual cells, in turn, *the two factors become completely separated or segregated from one another*, each of the new gametes containing either the one or the other but *never both.* This is well illustrated by the example which has been used here. The factors for purple and for white flower color both must be present in the F_1 hybrid, though only the purple expresses itself visibly in the plant. Out of this purple hybrid, when self fertilized, come some perfectly pure white plants which exhibit no trace of purple in their

* The first generation following a cross is known technically as the F_1 (first filial generation), the second as the F_2, the third as the F_3, and so on.

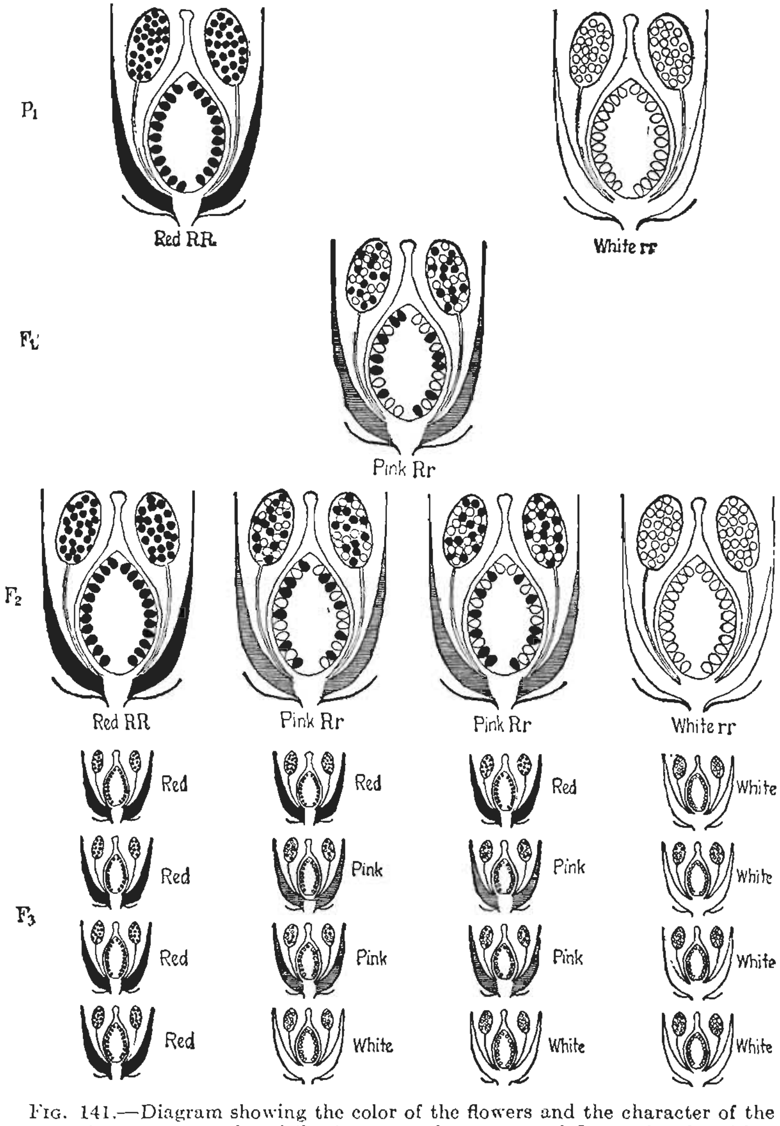


FIG. 141.—Diagram showing the color of the flowers and the character of the gametes in three generations following a cross between a red-flowered and a white-flowered plant where (as in snapdragon) the dominance of color is not complete. The gametes are represented by pollen grains and ovules, the black ones carrying the factor for red and the white ones that for white. In the F_1 the dominance of red is not complete and the flower is pink (shaded); but of the F_1 gametes half carry red and half white, and *none carry pink*. In the F_2 one-fourth of the plants are red-flowered and all their gametes carry the factor for red; one-half are pink-flowered, with half their gametes carrying the factor for red and half that for white; and one-fourth are white-flowered, their gametes all carrying white. The character of the offspring of these F_2 types, when self-fertilized, is shown in the F_3 generation.

descendants and some purples which exhibit no trace of white, thus proving that the factors for these characters, which for a generation have been existing together in every cell of the hybrid plant, have now (in one-half of the individuals) become completely separated and have not produced the slightest effect on one another.

The Genotype.—The relation between this fact of segregation and the actual results which are obtained in crosses is perhaps explained best if the factorial make-up of the plants and of their gametes is represented by simple letters or formulas (Fig. 142) in somewhat the same way that Mendel did in his original work. Every individual in a sense is a *double* structure, since it arises from the union of two gametes and draws half of its inheritance from one and half from the other. If *C** represents the factor for purple flower color and *c* the factor for white flower color, the pure purple-flowered parent, which received the factor *C* from both of its parents, may therefore be represented by the formula *CC*; and the pure white-flowered parent in the same way by *cc*. This formula applies to every body cell of the plant. Of course it should be borne in mind that these symbols represent only one of the great number of factor pairs which are present in the constitution of the individual.

In the cell divisions just preceding the formation of the gametes, there is a reduction by half in the amount of hereditary material contained in the nucleus† and every gamete produced now carries just *half* of each of the factor pairs which composed the parent plant. The gametes of the purple-flowered parent in the above illustration would therefore all be represented by the formula *C* and those of the white-flowered one by *c*. When these two plants are crossed and an egg, *C*, is fertilized by a male cell, *c* (or *vice versa*), the genetic formula of the resulting hybrid plant is obviously *Cc*. Since purple is almost completely dominant here, this plant *appears* purple-flowered, but in its factorial make-up (technically known as its *genotype*) there is a recessive factor for white. If dominance were absent and the hybrid were inter-

* It is convenient to represent a dominant factor by a capital letter and the recessive member of this factor pair by the corresponding small letter.

† The chromosomes of the nucleus in all probability are the actual bodies in which the genetic factors are carried, and in the *reduction division* just preceding the production of gametes, the number of chromosomes in the nucleus is halved (see page 390).

mediate in appearance—pink, perhaps—it would still be represented, of course, by exactly the same genotype. When the two members of a given factor pair are alike (as in each of the parent plants between which this cross was made), the individual is said to be *homozygous* for the factor in question; when the two members are different (as in this hybrid) it is said

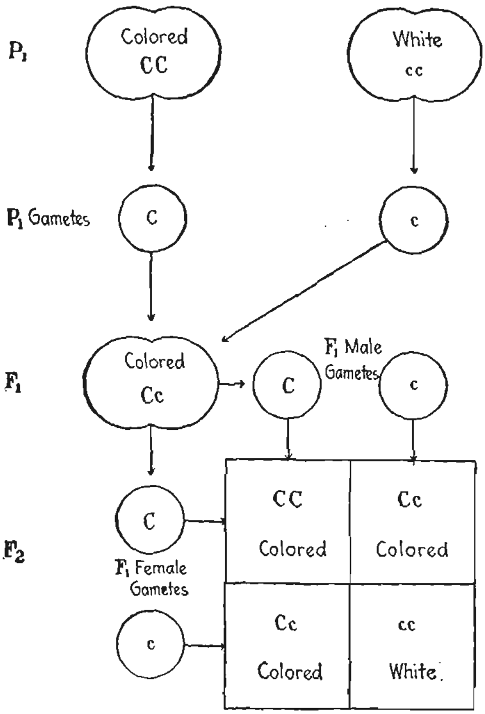


FIG. 142.—Chart showing the behavior of the factors for flower color in peas and giving the appearance and the genotypes of parents and F_1, the gametes which they produce, and the random union of F_1 gametes to form the three classes of F_2 plants shown in the checkerboard.

to be *heterozygous.* Now the essence of the phenomenon of segregation lies in the fact that when this heterozygous individual produces gametes, *these* are not hybrid or heterozygous at all, but half of them carry *C* and half *c*. Thus the hybrid character of a plant cannot be carried by its gametes, which must be entirely one thing or entirely the other. The factors *C* and *c*, brought in from the original purple and white parents, have co-existed in the hybrid without influencing each other in the

least and have now sharply parted company, or become segregated.

Mendelian Ratios.—In a cross between two of these hybrid F_1 plants (or in the case of a self-fertilization of one of them) the occurrence of the $\frac{3}{4}:\frac{1}{4}$ ratio in the F_2 generation is thus easy to explain. Of the gametes of each hybrid parent, approximately half carry the factor *C* and half the factor *c*, so that in the perfectly free and random union which apparently takes place between these gametes there are four possible combinations which may occur in the offspring produced. *C* male cells may fertilize *C* eggs, producing *CC* plants; *C* male cells may fertilize *c* eggs, producing *Cc* plants; *c* male cells may fertilize *C* eggs, also producing *Cc* plants; or *c* male cells may fertilize *c* eggs, producing *cc* plants. Each of these combinations, on the basis of pure chance, is likely to occur just as often as any other. Approximately one-fourth of the new generation, the *CC* plants, not only will look purple but will breed just as truly for this color as did their purple-flowered grandparent; approximately one-half, the *Cc* plants, will also look purple (perhaps somewhat paler) but are of course heterozygous, and when selfed or when crossed among themselves will behave just as did their parent, the F_1 hybrid, and yield approximately three-fourths colored-flowered plants and one-fourth white; and the final quarter, comprising the *cc* plants, will appear white and will breed as truly to this color as did their white grandparent (Fig. 141). The characteristic monohybrid Mendelian ratio therefore really is not $\frac{3}{4}:\frac{1}{4}$ at all (which accurately states the visible result when dominance is operative); but rather $\frac{1}{4}:\frac{1}{2}:\frac{1}{4}$. Of course it should be remembered that the results of actual breeding do not always display these ratios exactly, any more than in the tossing of coins or the throwing of dice there always are exact and predictable results. The ratios merely indicate what may be expected on the basis of probability, but do not make possible an accurate prediction of the character of any particular individual.

Obviously when dominance is absent the F_2 generation will not include simply two sorts of plants, one three times as numerous as the other, but a third, as well. A crimson snapdragon, for example, when crossed with a white one gives a *pink* F_1 hybrid. When selfed, this produces an F_2 in which approximately one-fourth of the plants are crimson (homozygous), one-half pink (heterozygous), and one-fourth white (homozygous), the $\frac{1}{4}:\frac{1}{2}:\frac{1}{4}$

ratio which has been mentioned just above (Fig. 140). It is evident that *pink* here is not a true Mendelian character at all, in the sense that it is inherited and will segregate, but that it is merely the expression of two factors in a heterozygous condition.

Independent Assortment.—When Mendel studied the inheritance of two or more factors simultaneously, he discovered the further important fact that segregation which takes place between the members of any one factor pair *is quite independent of that which takes place in any other,* so that in the second generation from the cross all sorts of recombinations, many of them quite unlike those found in the original parents, may occur. Let it be assumed that a plant which is homozygous for purple flowers and also for smooth seeds, and which therefore may be represented by the formula *CC SS*, is crossed with a plant homozygous for white flowers and also for wrinkled seeds, *cc ss*. The formula of the F_1 hybrid offspring of course would be *Cc Ss* and, as smooth seed coat is dominant over wrinkled, this plant would look like the purple-flowered, smooth-seeded parent. When gametes are formed by this plant, half of them carry the factor *C* and half the factor *c*. But it is clear that every sexual cell must carry within itself not only the factors for flower color but also those for seed surface and for all other plant characters as well; and half of the gametes must thus carry the factor *S* and half the factor *s*. Now in any given sexual cell, it seems to be purely a matter of chance as to whether the factor for purple flowers is associated with that for smooth seeds or with that for wrinkled seeds. The particular combination of factors which enters the F_1 plant from each parent (purple with smooth and white with wrinkled, in this case) has no effect whatever upon the way in which they are associated in the gametes produced by this plant. Their *assortment is independent.* Such a plant as the F_1 hybrid in this example will therefore produce four kinds of gametes in equal numbers: *CS*; *Cs*; *cS*; and *cs*. If two such plants are crossed, there will be *sixteen* possible combinations among their sexual cells, for there will be four kinds of pollen grains and four kinds of egg cells and union is quite at random. Any one of these combinations is as likely to occur as any other, and the sixteen types thus will tend to be equally numerous. Since two of these characters are dominant, the sixteen types will not all be visibly distinguishable, for the hybrids or heterozygous plants will resemble the pure dominants. The parents

and the F_1 and F_2 generations are shown in Fig. 143. The expectation in such a population evidently is that nine-sixteenths

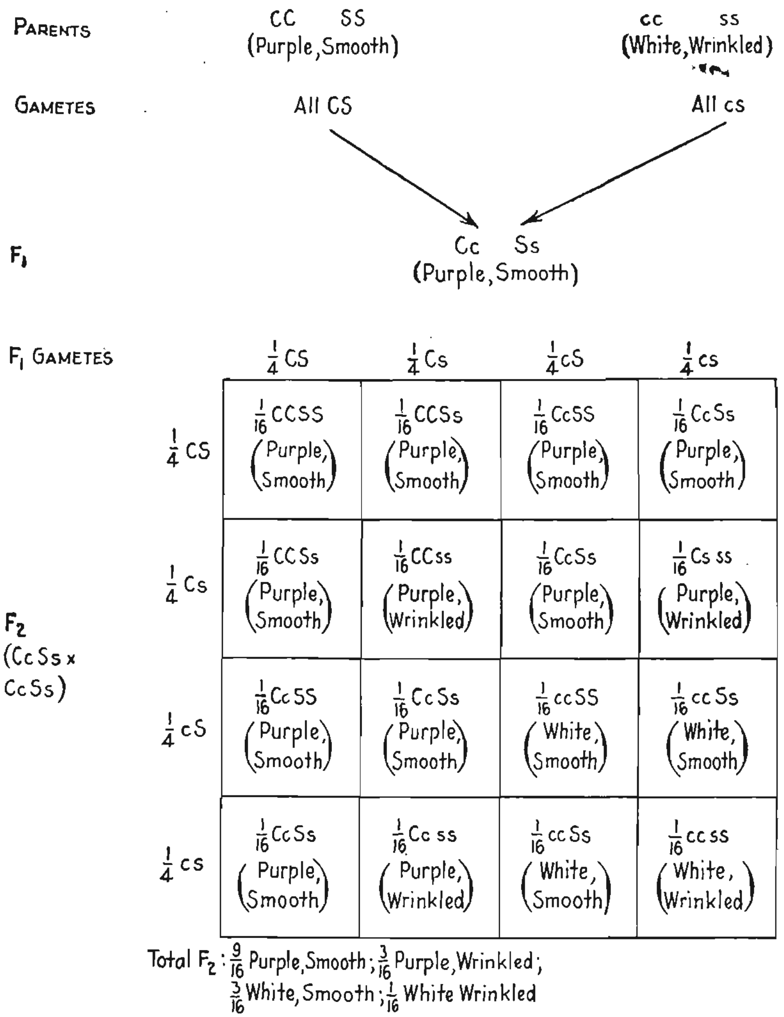


FIG. 143.—Diagram showing the appearance and the genotype of parents, F_1, and F_2 in a cross between a purple-flowered, smooth-seeded pea plant and a white-flowered, wrinkled-seeded one.

will show both dominant characters, three-sixteenths one dominant and one recessive, three-sixteenths the other combination of dominant and recessive, and one-sixteenth, both recessive char-

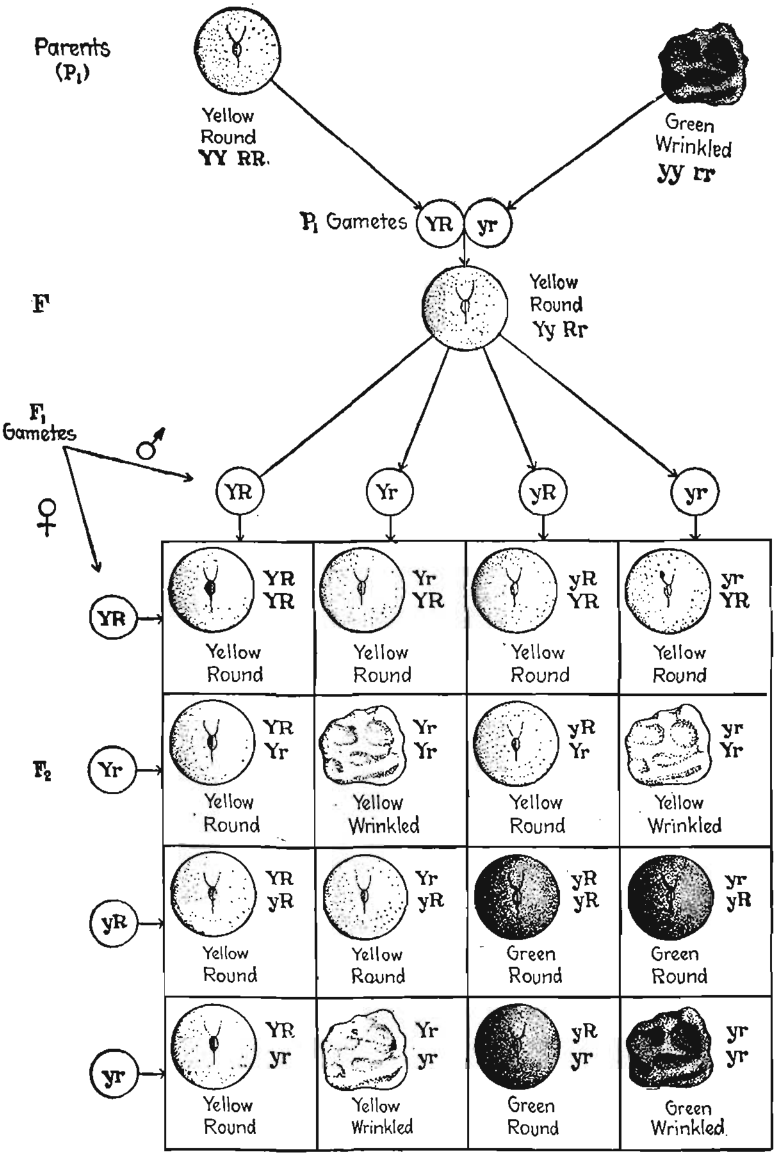


FIG. 144.—Diagram showing the appearance and genotype of parents, F_1, and F_2 in a cross between a yellow-seeded, round-seeded pea plant and a green-seeded, wrinkled-seeded one.

acters. The results of other such *dihybrid* crosses are given in Figs. 144 and 145 and show the characteristic ratio of $\frac{9}{16}:\frac{3}{16}:$

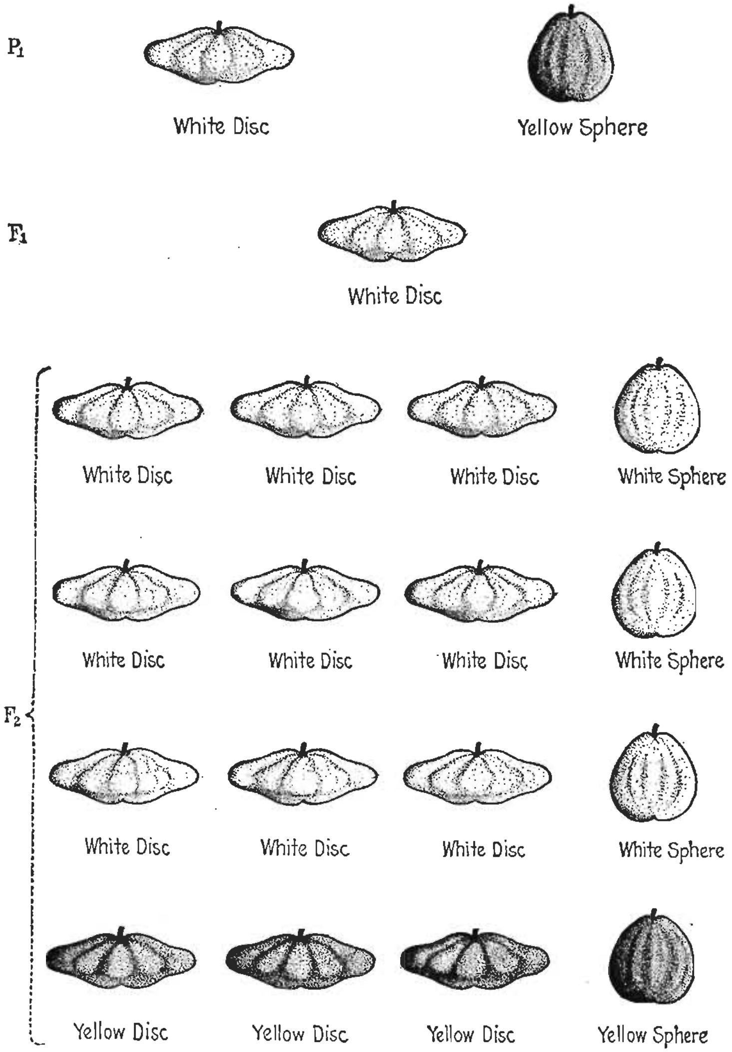


FIG. 145.—The appearance of parents, F_1, and F_2 in a cross involving fruit color and fruit shape in squashes.

$\frac{3}{16}:\frac{1}{16}$. The method by which new combinations of characters are secured through hybridization is thus clear; but it must be remembered that many of the F_2 plants are heterozygous in

one or both factor pairs and so will not breed true to their present appearance. The only F_2 individuals which will persist unchanged when inbred are those which are completely homozygous.

Complexities of Factor Expression and Interaction.—Such, in brief, are the essential features of simple Mendelism, the fundamental points of which are embodied in the principles of segregation and independent assortment. The intensive research of the past thirty years in the fields of both botany and zoology has shown that conditions in many cases are not as simple as Mendel found them in garden peas. A single character is often

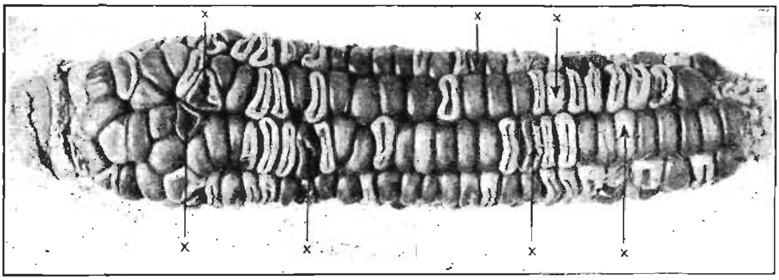


FIG. 146.—Linkage of characters in corn. Colored kernel is dominant over white and full over shrunken. If a white, full plant is crossed with a colored, shrunken one, and the F_1 crossed back on a white, shrunken plant, a result like the one here shown is obtained. Note that almost all the white seeds are full, and the colored seeds, shrunken, the same combinations as those brought in by the parents. There are a few *crossover* kernels (colored full, and white shrunken) which are marked on the photograph. (*From Hutchison.*)

determined by two factor pairs, or even a whole series of them, which may display various interactions in expression and thus render the inheritance of that particular trait a very complex affair, as is the case with kernel color in corn, flower color in snapdragons, and many others. Conversely, many factors affect not merely a single character but a whole series of traits throughout the body of the organism. Thus a factor producing pigment in the flower may also affect the color of the stem and the leaves. Certain factors, like that for albinism (lack of chlorophyll) in corn, ultimately cause the death of the plant and are said to be *lethal* in their effect, and may express themselves often merely through the non-appearance of certain classes of offspring. These various complexities, however, have been satisfactorily explained by amplifying and extending Mendel's laws of Segrega-

tion and Independent Assortment, which are now recognized to be among the most profound generalizations of biological science.

Linkage and the Chromosome Theory.—Certain characters, however, do not segregate independently, but instead tend to

FIG. 147.—A mutation in tobacco. The Stewart Cuban variety, which is very tall and produces an unusually large number of leaves per plant, originated as a mutation.

stay together in the passage from one generation to another, and thus constitute definite exceptions to the second of Mendel's main laws (Fig. 146). This *linkage* of traits has thrown much light on the actual physical basis of inheritance, since the number

of groups of linked factors has been found to correspond with the number of pairs of chromosomes in the nucleus, a fact which led to the theory now generally accepted that genetic factors (now more commonly called *genes*) are located in the chromosomes, and that it is entire chromosomes, rather than single factors, which show independent assortment. The linkage between two characters is explained on the assumption that their genes are carried in the same chromosome; and it is even possible to determine with

Fig. 148.—The "weeping" form of the European beech, which probably arose from the normal type by mutation.

some accuracy the location of these genes in the chromosome relatively to one another. Through the construction of such *chromosome maps* and the intensive development of this chromosome theory of inheritance, genetics has thus made indirectly a very valuable contribution to a knowledge of the constitution of living matter itself.

Mutation.—Certain types of variations are produced directly by differences in the environment to which the plant is subjected, and such are apparently never inherited. Another and doubtless a very common cause of variation is the segregation and recombination of traits which follow the crossing of two different

types; and these variations, being due to differences in the inherent genetic factors themselves, are clearly inheritable according to definite laws and are thus of the utmost importance to breeders. There is still a third type of variation, however.

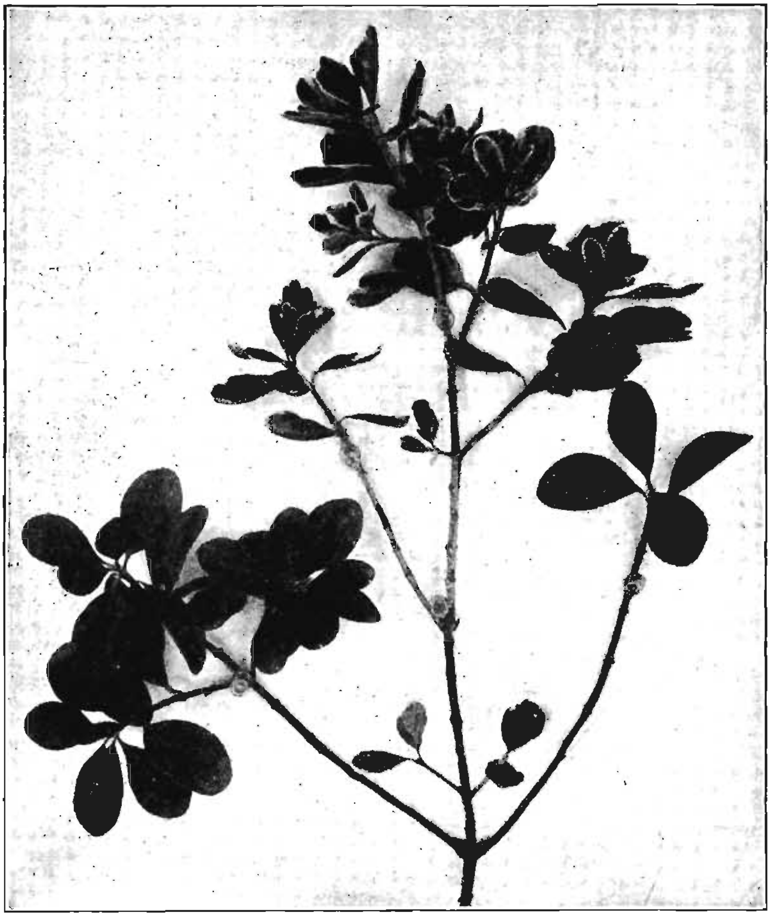


FIG. 149.—Bud mutation, showing variegated leaves, in a branch of *Euonymus*. (*From Shamel.*)

Frequently an individual clearly different from the rest will appear in a pure race where there apparently is nothing in the ancestry which can explain its origin, and will transmit this new character to some or all of its offspring. Such suddenly-appearing types are called *mutations* (Fig. 147). Many double-flowered

races of plants have arisen in this way, as have forms with cut leaves, white flowers, dwarf habit, weeping stems (Fig. 148), and many similar traits. When the history of such a group of plants can be traced, it often is found to have begun with a single individual which arose by mutation from the normal race and has transmitted its character to its descendants. In some cases a mutating individual is strikingly different from the normal type and then is often called a "sport." In others, the difference is so small that it can hardly be recognized. Most mutations show themselves in offspring grown from seed, and thus have evidently arisen in the reproductive cells themselves. Others are found in single branches or definite portions of the plant body, and since they evidently occurred here in a single bud, are called *bud mutations* (Fig. 149). All mutations agree in appearing suddenly and being transmitted to offspring, but the cause of their origin is still very obscure. It is sometimes possible to increase the production of mutations by artificial means, such as radium, X-rays, chemical agents, or low temperatures, but this at best is very difficult and uncertain. The plant breeder can understand and manipulate, to a certain extent, the variations due to environment and to hybridization, but as yet mutations are largely beyond his control.

QUESTIONS FOR THOUGHT AND DISCUSSION

509. What is the chief practical importance of discovering laws of inheritance?

510. In studies of inheritance in the summer squash it has been found that white fruit color is dominant over yellow, and that the difference between these two colors is due to a single factor. If a plant homozygous for white is crossed with a plant homozygous for yellow fruit color, what will be the appearance of the F_1 generation? of the F_2 generation derived by self-fertilizing one of these F_1 plants? What proportion of the white-fruited F_2 plants will breed true if self fertilized?

511. What will be the fruit color of the plants produced by crossing one of the F_1 individuals, mentioned in Question **510**, with its yellow-fruited parent? with its white-fruited parent?

512. Let the factor for white fruit color in the squash be represented by *W* and that for yellow by *w*. What kind of gametes, so far as their factors for fruit color are concerned, will be produced by plants having the following genotypes: *WW*; *Ww*; *ww*?

513. What gametes will be produced by the plants involved in the four following crosses; and what will be the fruit color of the offspring from each cross:

$$Ww \times ww;\ ww \times WW;\ WW \times Ww;\ Ww \times Ww?$$

514. A white-fruited squash plant when crossed with a yellow-fruited one produces offspring about half of which are white and half yellow in fruit color. What are the genotypes of the parent plants?

515. If the white-fruited parent plant in the preceding question is self-fertilized, what will be the fruit color of its offspring?

516. If this same white-fruited parent is crossed with one of its white-fruited offspring mentioned in Question **514**, what chance is there of obtaining from this cross a yellow-fruited plant?

517. Two white-fruited squash plants when crossed produce about three-fourths white and one-fourth yellow offspring. What are the genotypes of these two parents, as to fruit color? What will each produce if crossed with a yellow-fruited plant?

518. A cross between a white-fruited and a yellow-fruited squash plant produces offspring all of which have white fruits. If two of these F_1 plants are crossed together, what will be the fruit color of *their* offspring?

NOTE.—In four-o'clock flowers, red flower color is incompletely dominant over white, the hybrids being pink-flowered.

519. If a red-flowered four-o'clock plant is crossed with a white-flowered one, what will be the flower color of the F_1? of the F_2? of the F_1 crossed back on the red-flowered parent? of the F_1 crossed back on the white-flowered parent?

520. In four-o'clock flowers, let R represent the factor for red flower color and r the factor for white. What will be the flower color of the offspring from the following four crosses, in which the parents' genotypes are given:

$$Rr \times RR;\ rr \times Rr;\ RR \times rr;\ Rr \times Rr?$$

521. If you wanted to produce four-o'clock seed *all* of which would yield pink-flowered plants when sown, how would you do it?

522. In what respect is a character which behaves like flower color in Four-o'clocks easier to deal with in breeding work than one which behaves like fruit color in squashes?

NOTE.—In the inheritance of fruit shape in summer squash it has been found that the "disc" type is dominant over the "sphere" type (see Fig. 145).

523. In a cross between a squash plant homozygous for yellow fruit color and disc fruit shape and a plant homozygous for white fruit color and sphere fruit shape, what will be the color and shape of the fruit in the F_1? What will these be in the F_2 produced by crossing two of these F_1 plants together?

524. If one of the F_1 plants in the preceding question is crossed back on its yellow disc parent, what will be the color and shape of fruit in their offspring?

525. Let *D* represent the factor for disc fruit-shape and *d* the factor for sphere. What will be the color and shape of fruit in offspring of the following crosses:

WWdd × *wwDD*	*WwDd* × *Wwdd*
WwDD × *wwdd*	*WwDd* × *wwdd*
WwDd × *WwDD*	*WwDd* × *WwDd*

NOTE.—In the following six questions, all of which deal with fruit color and shape in the summer squash, the appearance of parents and offspring is stated. Determine in each case the *genotypes of the parents.*

526. White disc crossed with yellow sphere giving one-half white disc and one-half white sphere.

527. White sphere crossed with white sphere giving three-fourths white sphere and one-fourth yellow sphere.

528. White disc crossed with yellow sphere giving one-fourth white disc, one-fourth white sphere, one-fourth yellow disc, and one-fourth yellow sphere.

529. White disc crossed with white sphere giving three-eighths white disc, three-eighths white sphere, one-eighth yellow disc, and one-eighth yellow sphere.

530. Yellow disc crossed with white sphere giving all white discs.

531. White disc crossed with white disc giving 28 white disc plants, 9 white sphere plants, 10 yellow disc plants, and 3 yellow sphere plants.

532. A cross between a plant with white disc fruits and one with yellow sphere fruits gives 25 plants with white disc fruits, 26 with white

sphere, 24 with yellow disc, and 25 with yellow sphere. If the white disc parent is self-fertilized, what proportion of its offspring will have yellow disc fruits?

533. Explain how it can be that plants which look exactly alike may breed very differently.

534. Hybrid animals and plants notoriously fail to breed true. Explain.

535. If a potato breeder desires to obtain a new variety of potatoes by selection from among a large number of plants, would you advise him to plant potato "seed" (pieces of the tuber) or real seed from the seed capsule, to provide plants from which he may select? Explain.

536. Do you think that the characteristics of the fruits of an apple tree will be affected by the kind of pollen which fertilized the flowers? Explain.

REFERENCE PROBLEMS

139. Summarize briefly the life and work of Mendel and tell how his discoveries were finally brought to the attention of the scientific world.

140. Give examples (aside from those mentioned in the text) of several new plant varieties which have originated as a result of hybridization· as a result of mutation.

141. Name five varieties of cultivated plants which have recently been developed by plant breeders and which have proven particularly successful.

142. For some cultivated plant, compile a list of traits of which the method of inheritance has been established.

143. What is the Mendelian interpretation of the phenomenon of reversion or atavism, often observed by breeders?

144. What subjects are included in the science of Biometry?

145. In general, how do *quantitative* characters, such as those of size, weight, or number, differ in the manner of their inheritance from *qualitative* ones, such as color?

146. What are *multiple allelomorphs?*

147. State briefly why it is that the chromosomes, rather than any other part of the gametes, are believed to carry the hereditary factors.

148. What is a *pure line* of plants? Of what importance are pure lines in agricultural practice?

149. Under what conditions is selection effective in causing a permanent change in type, and under what conditions is it ineffective?

150. What is meant by "bud selection" in horticultural practice?

151. Give author and title of three important books on genetics, and outline briefly the content of each.

152. Name several botanical investigators who have done important work in plant genetics, and state the notable contributions made by each.

153. Give the derivation of the following terms and explain in what way each is appropriate:

Heredity	Segregation	Mutation
Allelomorph	Homozygous	Genotype

CHAPTER XII

PLANT EVOLUTION

Among all organisms which can be watched carefully, new variations are continually appearing and being inherited. This fact at once suggests that living things are not constant and changeless in their characteristics but that they may undergo a certain degree of permanent modification as the generations succeed each other. A study of the remarkable development of domestic plants and animals, since man first began to utilize them and to improve them by selection, shows the possibilities of change which exist among organisms. The difference between the small, sour prototype of the apple, for instance, and the modern large and delicious varieties is so great that one hardly can recognize the relationship between the two. In fact, many cultivated forms have progressed so far under human guidance that it is not known what their wild ancestors really were.

Since the days of the Greeks, philosophers have often speculated as to the possibility that the whole organic world—plants, animals, and man—has reached its present state through a gradual evolution from far simpler forms, perhaps ultimately from inorganic matter. It is only within the past century, however, that the subject of evolution has descended from these clouds of speculation and become a problem for scientific study. Little by little, evidence has been accumulating that progressive change has actually taken place, and that the plants and animals which now exist differ radically from their ancestors in past ages. As to just how this has been accomplished biologists are still far from agreed; but as to the *fact* of evolution there now is no doubt in the minds of scientific men. An insistence that every species was specially and suddenly created in exactly the form which it now displays has given way to the conception of the world as the theatre of a slow but steady upward progress from lower to higher types of life.

Evidences for Evolution.—The lines of evidence on which the belief in evolution is based are various, and will be discussed briefly here.

Geological Evidence.—Probably of most importance is the existence of *fossils,* the actual remains or impressions left in the rocks by ancient plants and animals, caught and imbedded in the sand or mud millions of years ago. Fossils do not occur indiscriminately but similar types appear in rock layers which are known, from their position, to be of about the same age. Geologists are able to assign each rock layer, or stratum, to its particular level in the great series which records geological history from a very remote past to the present, and as one passes upward through this series, from the most ancient rocks to the

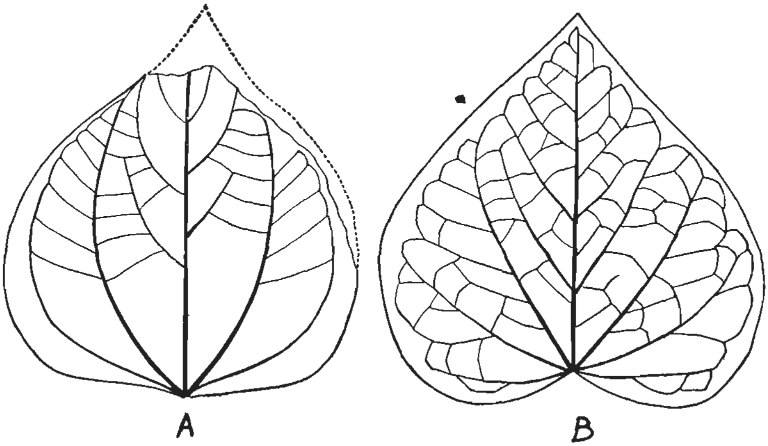


FIG. 150.—*A*, leaf of a fossil species of the Judas tree (*Cercis*), from the eocene of Tennessee. *B*, leaf of a living species, *Cercis canadensis*, now growing throughout the eastern United States. The two species are similar to each other but are clearly distinct. Our living species has probably been evolved from an ancestor much like the fossil one here shown. (*After Berry.*)

most recent ones, he finds that the fossil remains undergo progressive change, older types becoming extinct and newer ones appearing; and that as modern times are approached, the prototypes of familiar plants and animals begin to come into view (Figs. 150 and 151) until in recent deposits there occur as fossils species which still exist. There are enormous gaps in this record but the advance of geological science is slowly filling them in, and even now a glimpse may be caught of the main scenes in the pageant of evolutionary progress. Among the members of the plant kingdom it is possible to witness the rise, luxuriance, and extinction of several great groups; to trace the development of seed plants from lowly, fern-like forms, and to recognize

approximately the point at which the higher seed plants or angiosperms first appeared upon the earth. Just how these successive groups were related in descent is, in some cases not altogether certain and must await further discoveries, but as to the main fact of progressive evolutionary advance in the character of the plant types there can be no doubt. No other evidence for evolution is quite so convincing as are these tangible remains of extinct organisms.

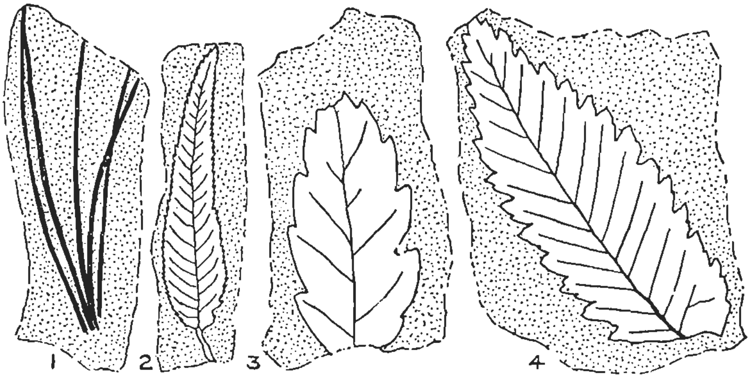


FIG. 151.—Fossil leaf impressions of miocene age from Colorado, very similar to living species. 1, pine; 2, willow; 3, oak; 4, elm. (*From Ramaley.*)

Taxonomic Evidence.—The general character and classification of the plant and animal kingdoms also bear testimony that their present state is the result of descent, with progressive modification, from earlier types. A study of the external and internal structure of living things makes it clear that they are not haphazard and random in their characteristics, but that they fall into well-marked *groups* of similar forms, the members of which show definite resemblances to each other. All similar individuals are classed together as a species. A number of species resemble one another so much, and are usually so different from anything else, that they are placed together as a *genus*. A number of genera, in the same way, stand apart as a *family*. Families are united into orders, orders into classes, and so on. It is possible to understand this grouping of similar species and their union into progressively larger aggregations if the organic world is regarded as a huge "genealogical tree," its members related to one another—some nearly, some remotely—by ties of descent, the "twigs" representing species, which unite into larger and

larger branches as they are traced back to the main trunk. It is assumed, for example, that all the various species of rose, which stand apart as a definite group or genus, have descended from a common rose ancestry, perhaps a single individual; that the roses, apples, blackberries, spiraeas, and other rosaceous plants, which today form a definite family, have all had a common ancestor, the remote progenitor of the rose family as a whole; and so on to the larger and larger aggregations. The fact that organisms occur in groups subordinate to groups, and can thus be classified readily, makes possible the science of taxonomy, and is very difficult to explain except on the theory of evolutionary descent with progressive modification.

Morphological Evidence.—Equally significant are certain facts which morphology presents. Characteristic similarities in type of leaf venation, relation of floral parts to one another, size and shape of wood rays, and many other morphological traits often occur throughout whole families or even larger groups. The butterfly-like or papilionaceous flower in the legume family, and the characteristic pitch canals in the wood of the pine and its allies may be cited as examples. Such traits serve to distinguish one group from another, and are therefore useful in taxonomy, but it is very hard to explain this restricted distribution which they display unless one assumes that all the members of a group which shows such a character have descended from a common ancestor in which the trait first made its appearance.

Furthermore, many organs exist today in a state evidently useless to the plant or animal possessing them, and for these it is hard to account unless they are looked upon as vestiges or remnants of structures which once had a use but have lost it during the course of evolution. Vestigial stamens, petals, sepals, stipules, and leaf blades, as well as various functionless internal structures, are of frequent occurrence in plants, and there are many similar instances in the animal kingdom. Their presence can be explained only on the assumption that they once were well developed and functional but that evolutionary progress, which makes them necessary no longer, has resulted in their gradual degeneration.

Evidence from Geographical Distribution.—Impressive evidence in favor of evolution is presented by the facts of geographical distribution. Most plant species, in their wild state, are not widely dispersed over the earth's surface, or even over that

part of it in which conditions are well suited for their growth. The golden-rods, for example, are practically confined to North America, the eucalypts to Australia, the tobaccos to the western hemisphere, and so on. Such localized distribution can well be

FIG. 152.—Three of the four species of *Sabatia* the distribution of which is mapped in Fig. 153. They are quite distinct from one another. 1–3, *Sabatia Kennedyana;* 4 and 5, *S. dodecandra;* 6–8, *S. decandra.* (*From Fernald.*)

explained only on the assumption that these plants actually were evolved in the regions which they now inhabit, and have been confined there ever since by barriers of various sorts. The distribution of the four closely related species of the coastal-plain genus *Sabatia* (Fig. 152), which is mapped in Fig. 153, is an excellent examples of this sort of geographical evidence. These species

now occupy almost a continuous area from Florida to Nova Scotia, but their ranges overlap hardly at all. Such a distribution can be understood most easily on the hypothesis that all four have descended from an ancestor which occupied much or all of the present range of the group, and that through the appearance

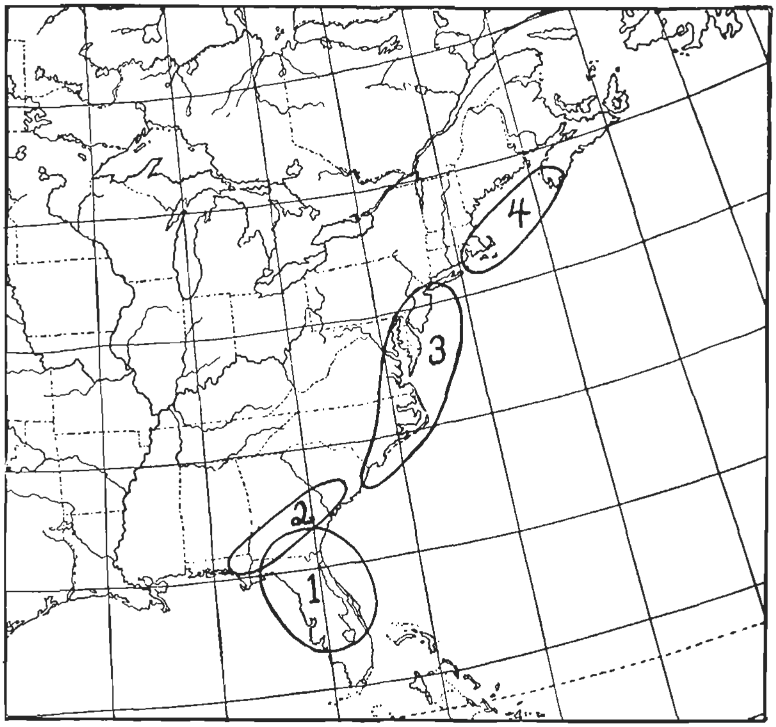


FIG. 153.—The distribution of four closely related species belonging to the same genus (*Sabatia*, section *Pleienta*). 1, *Sabatia decandra*. 2, *S. foliosa*. 3, *S. dodecandra*. 4, *S. Kennedyana*. These four very similar but readily distinguishable species have presumably all evolved from a common ancestor, which once grew on the coastal plain of southeastern North America. (*Data from M. L. Fernald.*)

of local varieties adapted to particular local conditions, and the gradually increasing differences between these varieties, the original species finally lost its identity and became divided into four new but closely related species.

An earlier stage in such an evolutionary process is shown by *Gaylussacia dumosa* and its variety *Bigeloviana* (Fig. 154). The former ranges from New York south to the Gulf, the latter from

New Jersey to Newfoundland. This group is still relatively uniform, the difference between its two components not yet having become sufficiently marked so that taxonomists are willing to call

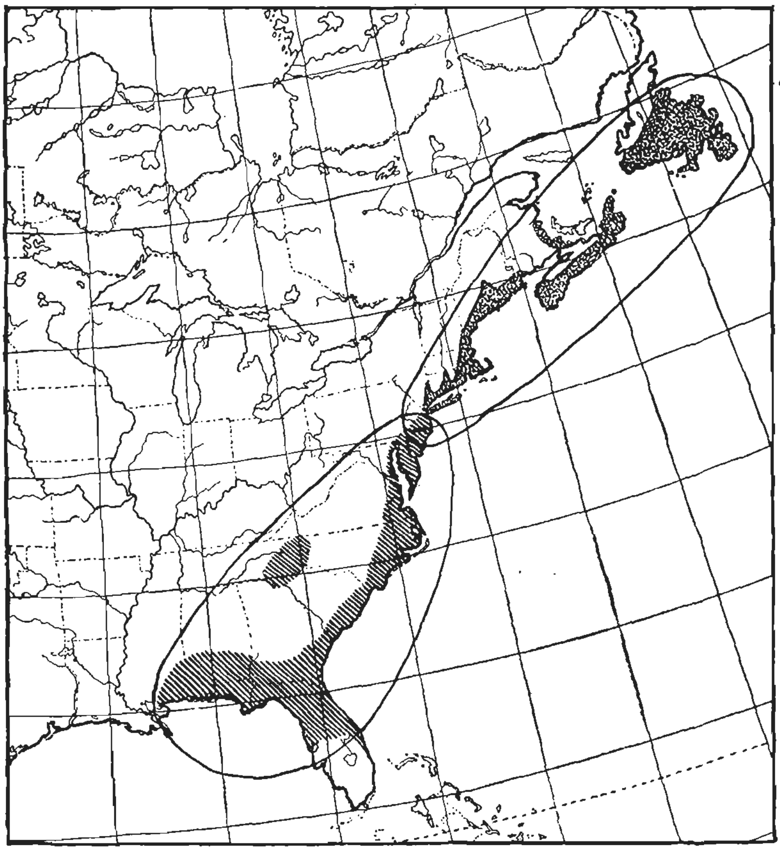


FIG. 154.—The distribution of *Gaylussacia dumosa* (lined) and its variety *Bigeloviana* (dotted). The species is characteristically southern, the variety northern. In New Jersey and adjacent Pennsylvania, where their ranges overlap, the variety merges into the species, but in the rest of its range it is quite distinct. Here are evidently two groups of plants, within a single species, which occupy different regions and which have diverged from one another almost far enough to be regarded as two distinct species. (*Data from Fernald.*)

them distinct species. It is easy to see, however, that the northern form and the southern one, largely isolated from each other and growing under different conditions, are likely in the not very remote future (geologically speaking) to attain a degree of distinctness equal to that now shown by the species of *Sabatia.*

Cases like this seem to be examples of species actually in the making. As to the causes which lie behind such changes there are differences of opinion, but that the changes are occurring seems open to little doubt. The same phenomena occur repeatedly throughout the animal kingdom, and it is certain that the great mass of facts at hand as to the geographical distribution of organisms would largely be unexplainable except for the belief that each species, genus, and family of plants and animals has had its place of origin from ancestral forms and its own individual evolutionary history.

Experimental Evidence.—The most convincing evidence that evolutionary change is taking place would, of course, be the actual observation of the origin of new types of living things in nature, but the process seems to be such a slow one, and the time since careful observations began to be made is relatively so short, that no information of very much value has been obtained in this manner. Experimental studies upon plants and animals, however, and particularly investigations dealing with variations and their inheritance, have given strong support to the theory by making clear that living things are not fixed and unchangeable in type, and by indicating how readily evolutionary change might take place among them.

In the preceding chapter it has been shown that variations (aside from those caused by the environment) may arise either through the recombination of mendelian factors or by mutations; and that these variations are inherited according to definite laws. In species which have been longest under laboratory observation, hundreds of mutations have been observed, and in a few cases this change has progressed so far that forms have resulted which, to all intents and purposes, are actually new species and would certainly be so considered if found in nature. It is with the method rather than the accepted fact of evolution, however, that these studies in experimental evolution are chiefly concerned.

Because of such evidence as has been presented here, the scientific world has become convinced that evolutionary change actually has occurred and that the familiar plants and animals of today are the most recent members of innumerable lines of descent, reaching back for millions of years and embracing a multitude of ancestral forms long since extinct and differing from anything now alive.

An admission of the fact of evolution at once raises two difficult questions, however: whence came the first living thing, the original ancestor of all which have since evolved; and what has been the *cause* of this steady and long-continued evolutionary progress? The first question involves the origin of life, about which one frankly must admit that man's ignorance is still complete. The second, which relates to the cause and method of evolution, is more nearly answerable and has been the subject of intense interest and close study for more than a century. Indeed, it was an inability to explain why and how evolution might have taken place that for so long prevented a general acceptance of the belief that it really had occurred at all. Although much progress has been made in this field of inquiry, biologists are still far from a complete and convincing solution of the many problems which the study of evolution has raised.

Lamarck's Theory. The Environment.—The first modern theory which attempted to explain evolution was put forward by the great French biologist Lamarck (Fig. 155) about 1809. He was much impressed by the profound effect which the environment produces and noted many instances of its operation, such as the vigor and luxuriance of plants growing in rich soil as contrasted with their stunted growth where the soil is poor (Fig. 136). In the cases of several "amphibious" species he observed that leaves produced when the plant is growing under water are very different from those formed in the air (Fig. 93). He also observed the great structural changes which are brought about, in animals, by the use or the disuse of an organ. Lamarck believed that organisms possess the ability to react to their environment advantageously and to modify their structures and functions in such a way that success under a changing environment will be attained. He never questioned that all the variations which he noted were transmitted directly to offspring by heredity, and he thus pictured the races of plants and animals as being pushed along the evolutionary road by environmental forces.

Lamarck's explanation, although very attractive and plausible in certain respects, has never won wide acceptance. Biologists as a rule have not been willing to admit that an organism has any innate ability to guide its reactions into a favorable course. The theory has suffered still more from the absence, after intensive search, of any very conclusive evidence that "acquired"

characters, such as those produced by the environment, are ever inherited. There are a few biologists today who believe that in certain of its features Lamarck's theory comes nearer to explaining the true method of evolution than does any other yet suggested, but as a whole it receives little support.

FIG. 155.—Jean Baptiste Lamarck (1744–1829). *(From A. F. Shull, after Locy.)*

Darwin's Theory. Natural Selection.—The most notable attempt to solve the riddle of evolution is the theory of Natural Selection put forward in 1859 by Charles Darwin (Fig. 4) in "The Origin of Species," a book which has had a very great influence on all human thinking. The effect of this theory in rendering the whole process of evolution plausible and understandable was the chief factor in convincing scientific men of the truth of the evolutionary theory in general; and whatever one may think today of the merits of some of Darwin's hypotheses, it must be recognized that the thoroughness of his scientific work and its revolutionary effect on all lines of biological thought entitle him to rank as the greatest exponent of evolution.

Darwin based the theory of Natural Selection upon three main facts: variations and their inheritance; over-production of offspring with consequent competition (the "struggle for exist-

ence";) and the elimination of the least favorable variations (the "survival of the fittest").

He was vividly impressed by the occurrence of variations in all animals and plants and studied them carefully, endeavoring to discover their causes. Like other scientific men of his day, Darwin did not understand clearly the mechanism and laws of inheritance. He believed, at least in his earlier work, that "acquired" characters might be transmitted to offspring, but this belief did not form the essential basis for his theory, as it did for that of Lamarck. The main fact which he emphasized was that variations in all directions are exceedingly abundant and that in many cases they certainly are transmitted by inheritance to the offspring.

The over-production of progeny in plants and animals forms the next step in the theory. If all seeds which are produced were to grow and if all animal young were to mature, there soon would be no room or food for them on the earth's surface. Only a small fraction can possibly live to maturity. As a result, argued Darwin, there necessarily must be a terrific life-and-death competition, in which the few survive and the many perish.

Finally, those individuals in this struggle which possess any advantage in structure or in function over their fellows, even if this advantage is a very small one, will evidently have the best chance to succeed and survive. Of the manifold variations which plants and animals display, some naturally will be helpful and some harmful, and those fortunate individuals which vary in the right direction will survive and will transmit their advantageous characters to their offspring. The others will perish and leave no descendants. Through this "survival of the fittest" the race tends to change steadily and to progress toward a type which is better and better adapted to the conditions under which it is living, and also to develop new types which can successfully invade new environments. Darwin named this process *Natural Selection* from analogy to the artificial selection long practiced by man with his domestic animals and plants, by which he has caused such great changes merely by selecting, for breeding stock or for seed production, those individuals which varied in such a way as best to meet his requirements.

It should, of course, be clearly understood (as often is not the case today) that the *theory* of evolution, and Darwin's *explanation* thereof by natural selection ("Darwinism") are

entirely different propositions. All biologists accept the former, but many are doubtful as to the complete adequacy of the latter.

Objections to Darwin's Theory.—In support of his theory Darwin brought forth a wealth of evidence so convincing that it won very wide acceptance. As knowledge has advanced, however, various objections to it have been persistently raised. Why is an advantageous character appearing in only one individual not lost, by "swamping," in crosses between this individual and the rest of the population? Why do so many structures exist which seem not to be helpful in survival? Why are many species separated by differences so small that it is hard to believe that they are life-and-death differences? What causes the persistence and survival of early steps in the development of a structure, before it has become perfected and can be useful to the organism? If variations occur at random, as Darwin supposed, how does it happen that a complex and highly coördinated structure could ever develop, since its production would require innumerable variations of just the right degree, in just the right place, and at just the right time? Why have breeders never been able to produce by artificial selection a group of individuals which could clearly be regarded as a new species?

These and other objections have been answered in whole or in part by Darwinians, but they still are of sufficient weight to convince most biologists that the theory just as Darwin left it cannot well be maintained today. No doubt natural selection eliminates vast numbers of obviously unfit individuals, but that it has been the sole factor in producing new forms, and thus in directing evolutionary progress, is now rather generally doubted.

De Vries's Theory. Mutation.—Another attempt to explain the cause and method of evolution has been made in recent years by the Dutch botanist De Vries, who believes that the small and almost imperceptible variations, regarded as most important by Darwin, are merely "fluctuations" around the normal type and have been produced by the environment, and that they are therefore not inheritable. The real variations which lead to evolutionary change, according to De Vries, are the *mutations*. These are permanent and inheritable, and are often large and conspicuous. The founder of the Mutation Theory thus looks upon organic nature as advancing by distinct

and usually rather long steps rather than by an almost infinite number of short ones.

Although De Vries recognizes the importance of natural selection in evolution, his theory has certain advantages over that put forward by Darwin. If complex new characters and even new varieties and species can arise by one or even a few steps, the problem of the preservation of the early stages in the development of a useful structure is partly solved, and the existence side-by-side of distinct but very similar species is explained. The length of time necessary for evolution is also reduced. Many of the objections which have been urged against Darwin's theory, however, apply with equal force to that of De Vries, and although the latter has emphasized the necessity of distinguishing sharply between inheritable and non-inheritable characters in evolution, it has not been accepted as a complete solution of the problem.

Hybridization and Evolution.—Another school of biologists are impressed with the increase in variability following a cross between individuals which differ from one another, particularly if these differences are considerable. This increase in variability, which has long been recognized as characteristic of the offspring of hybrids, is now explained readily as a necessary result of the operation of known laws of heredity. Hybrids between species or varieties have often been found in nature and doubtless occur with considerable frequency, especially in those groups where cross-fertilization is common; and it seems quite possible that much of the variability exhibited by plants and animals is the result of such natural hybridization. If only a few inheritable differences arise through mutations, these differences will appear in a great variety of combinations among the descendents from a cross involving them, owing to the segregation and recombination of traits which necessarily occurs in the offspring of heterozygous individuals. New types thus formed, particularly if they are more or less isolated, may perhaps develop into new varieties and species among which many of the differences would not be such as to affect survival. This explanation of evolutionary change, while not undervaluing the importance of natural selection in weeding out the manifestly unfit, meets certain of the objections raised against Darwin's hypothesis.

Orthogenesis.—These various theories lack a convincing explanation of the progressive appearance of new characters which are incorporated harmoniously into the organism. The

environment evidently cannot produce them, and it seems unlikely that mere random mutations and recombinations would be any more successful. In view of all this, some biologists have turned to the organism itself to discover the directive factor in the production of new forms. They believe that variation is not a random process but that in any given species, or succession of individuals, the variations tend always to be of a certain particular sort, characteristic of that species, and that the species consequently undergoes progressive change in a definite direction. The advocates of such a theory of *Orthogenesis*, or internally directed evolution, believe that evolutionary change is due to the unfolding of certain tendencies in the protoplasm of the plant or animal, and is not forced upon the organism from without. They recognize the importance of natural selection in eliminating the unfit, but believe this agency quite unable to create anything new or to produce the organic world as it is known today.

It must be admitted that as yet biologists do not fully understand the manner in which evolution has taken place and the factors which have been responsible for it. In the past there has been perhaps too much unsupported speculation on the problem and too little pursuit of facts. The present intensive experimental study of heredity, physiology, cytology, and morphogenesis will, it is to be hoped, make available a fund of information for further attack upon this important problem.

The Evolution of the Plant Kingdom.—In the plant kingdom this progressive evolutionary advance seems to have been taking place, slowly but steadily, for many millions of years, a period so enormously long that the entire human era seems but a moment in comparison with it. Biologists may disagree as to the exact causes which are responsible for evolution, but the results of this process are evident in the scores of thousands of plant species with which the earth is covered today. Those who are familiar only with the vegetation of the temperate zone, however thriving and vigorous this is, can have little idea of the luxuriance and variety of plant life exhibited in tropical and subtropical regions. In New England there are about 4000 species of seed plants, but probably more than 50,000 occur in Brazil, and in the whole world there already have been described a vast array of almost 250,000 species. Nor is our knowledge by any means complete, for although during the past three hundred years botanical exploration has been active in all parts of the

globe, the discoveries of new species are still constantly being reported. It is the seed plants which constitute the dominant and conspicuous part of this diverse plant population, and in the present volume attention has been confined almost exclusively to these, but one should remember that the plant kingdom includes a host of lower and simpler members. Of the ferns and their allies there now are known more than 4500 species, and in many parts of the earth they provide an important element in the vegetation. Of the liverworts and mosses there are some 16,000 species, and these are far exceeded by still lower forms, the fungi, with approximately 60,000 species, and the algae with 20,000. In all these groups, exploration and critical study are adding yearly many new forms, and it is probably safe to estimate that, were their knowledge complete, botanists would be able to recognize not less than 300,000 species of plants. The day has passed when any one person can hope to become familiar with more than a small portion of the flora of the globe.

That record of remote events which has survived to the present day in the form of fossil plants makes it clear that the panorama of the earth's vegetation has changed repeatedly, that group after group has arisen, flourished, and disappeared, and that thousands of species have evolved only to become extinct. Plants of today are the product of a long period of evolutionary development, and to understand the vegetable kingdom and its relationships one therefore must know something of the main events in its history.

Plants and Animals.—Plants and animals constitute the two great branches of the organic world. In their lowest representatives they are often hard to distinguish from one another, and certain simple forms exist which clearly combine the characters of both kingdoms. The earliest of living things would perhaps have been difficult to classify, but as evolution progressed, animals and plants became clearly distinguishable through the development among their members of certain characteristic traits. The animal tends to be motile, to ingest its food through a mouth, and to depend on other organisms as sources of food supply; the plant tends to be stationary, to absorb its nutrient materials in solution over a considerable area of the body, and (except in the fungi and a few others) to manufacture its own food from simple inorganic substances. Many other differences in

structure and function are associated with these fundamental ones.

Forward Steps in Plant Evolution.—During the divergent history of the two great groups, certain notable events took place in each with which the student of biology should become familiar. Before discussing the classification of the plant kingdom which follows in the succeeding chapters, it will therefore be useful to consider briefly a few of the important steps which have marked its evolution.

The causes which led to the appearance of life on the earth, and the characteristics which the earliest organisms displayed, are buried so deeply in antiquity that they probably never will be discovered. There is good reason to believe, however, that among the most ancient of plants, thriving in the warm primeval seas, were simple, single-celled forms which multiplied by simple division or *fission*, possessed chlorophyll or a similar substance, and in their general characters were not greatly unlike some of the simplest of living algae. For ages they doubtless were the only vegetable life on the globe.

The Multicellular Plant.—The first great forward step which, like all first steps, was probably long in its accomplishment, consisted of the union of these simple cells into colonies (Fig. 166). The two daughter cells formed at a division remained attached to one another instead of separating, and thus arose small cell groups or aggregations such as may still be seen among the lowest algae. The individual cells forming these groups might cohere variously—in spherical masses, in threads, or in sheets. Through a still more intimate union between their members these cell colonies gradually developed into definite *multicellular plants*, various in size and shape, and probably much like some of the simpler seaweeds of today. The way was thus opened for the production of those very large and complex plant bodies which are so conspicuous and familiar.

Differentiation.—The evolution of the many-celled plant was followed soon by another and equally important advance, the beginning of *differentiation* (Fig. 164). The primitive single cell performed all the functions which are now associated with the entire plant, such as absorption, photosynthesis, and reproduction. Soon after the multicellular individual had arisen, however, there began to appear within it the same tendency which manifests itself in the evolution of a human society, the "division

of labor." Instead of the primitive condition in which *all* the individual cells carry on *all* the functions, certain cells became specialists, some of them gradually assuming the performance of one function and some of another, and acquiring through this specialization a more or less conspicuous modification in structure. The first activity of plants thus to be localized was probably reproduction. Instead of a condition where every cell divided and gave rise to new individuals, certain ones were set apart to produce specialized reproductive cells or *spores*, provided with means of locomotion or other facilities which made them particularly well adapted to establish a multitude of new and widely scattered plants. This process of differentiation has progressed steadily during the evolution of the plant kingdom and has resulted in the marvelously complex individuals found in the higher groups. Here the various functions have *organs* devoted to their performance and in these the cells, far from being uniform, are grouped in definite and highly specialized *tissues*, each of which plays its particular part in the life of the whole. Differentiation has made possible the existence of the higher plants, and is one aspect of that phenomenon of *organization* or *regulation* to which attention has been called so often.

Sexual Reproduction.—Another important step in the history of the plant kingdom involved the method by which reproduction took place. In the earliest plants, this process was accomplished merely by a division of the cell into two. In forms a little more advanced, special cells became differentiated, each of which was able to produce a new plant. Following this stage, the type of reproduction known as *sexual* probably made its appearance. The essential feature of this method is the *fusion* of two cells into one and the subsequent development therefrom of a new individual (Fig. 159). The cells which unite thus are called sexual cells or *gametes*, and the product of their union the *zygote*. In early plants, the gametes were probably nothing more than the ordinary non-sexual reproductive cells which had assumed this additional function; and in some of the algae today are found cells of this sort, which may reproduce the plant either sexually or asexually. Soon the gametes became clearly distinct, however, and asexual reproduction was often given up, or resorted to only under special conditions. The sexual cells themselves became further differentiated into two sorts—small, active *male* gametes or *sperms*, and larger, non-motile *female* gametes or

eggs, a condition which now accompanies sexuality so commonly that instances of equal gametes are comparatively rare. The causes which led to the development of sexual reproduction are unknown, but the process is so nearly universal, not only among plants but throughout the animal kingdom, that it apparently must have some special significance. There is evidence that sexual fusion results in increased vigor, particularly when the two gametes come from different individuals; but many plants are also known which may reproduce indefinitely by various asexual processes without evident loss in vitality. A considerable proportion of the activities of plants, however, seems to be devoted to the successful accomplishment of the sexual process.

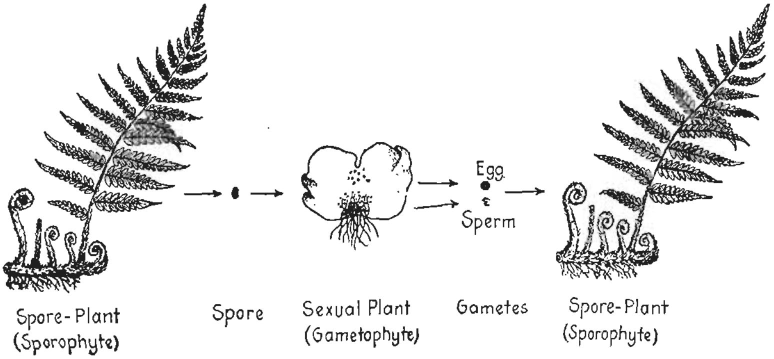


FIG. 156.—The alternation of generations in a fern.

Alternation of Generations.—These three steps in plant evolution—the appearance of the multicellular individual, of functional and structural differentiation, and of sexual reproduction—occurred also among animals. The fourth belongs exclusively to the plant kingdom. It is the evolution of that remarkable double life-cycle known as the *alternation of generations* (Fig. 156), a process simple enough in its underlying principle and in its expression among some plants, but which in other groups leads to such complexities that an understanding of the process of reproduction is more difficult in the vegetable kingdom than among animals. It is impossible to understand this process clearly until one is familiar with the life histories of representative members of the main groups in the plant kingdom, and its development can best be discussed in detail under these various groups.

In brief, it involves the occurrence of two distinct phases in the life history, each of which produces the other. One is the sexual phase or generation, the *gametophyte*, which bears male and female sexual organs and gametes and in which fertilization is effected. The fertilized egg does not develop into another gamete-bearing individual, however (as it does in animals), but into a non-sexual phase, the *sporophyte*, which does not bear sex organs but produces instead a large number of single-celled spores, each of which without any sexual process develops directly into a new gametophyte.

In the mosses (and certain of the lower forms) the gametophyte is the dominant and conspicuous generation and constitutes the "plant," the familiar long-stalked moss sporophyte being nothing more than a spore-bearing structure developing directly from the fertilized egg and attached to the body of the gametophyte. In the ferns and their allies, however, it is the sporophyte rather than the gametophyte which is large and conspicuous. Here it develops roots, stems, and leaves, and has become the dominant stage in the life history. This fern plant bears on the backs of its leaves enormous numbers of minute spores. Each of these, under favorable conditions, may develop into a small and inconspicuous but *independent* generation, the gametophyte or prothallus, on which the sex organs are borne. Here fertilization occurs and from this sexual union develops a young sporophyte which ultimately grows into the familiar fern plant again. In the seed plants the sporophyte is still dominant, but the sexual generation, instead of remaining independent and free-living, as in the ferns, has become very much reduced and is now borne in the tissues of the sporophyte.

This characteristic alternating type of life cycle is thus expressed in very different fashions in the various groups of the plant kingdom. In every case, however, the fundamental difference between a sexual and a non-sexual generation persists.

The Invasion of the Land.—The fifth great forward step in plant history was the evolution of a type able to grow in the air rather than in the water, and which thus made possible an invasion of the dry land and the establishment there of a real terrestrial vegetation. Plant life probably began in the sea. Here also, doubtless, took place the first great steps in the evolution of the vegetable kingdom; and although the seas teemed with life, the land masses of the earth were probably for a very

long period of time barren wastes, or at best covered in their damper spots only with a scum of algae. This great area was open freely to whatever plant pioneer should be able to master the difficulties of such an environment.

These difficulties were many and formidable. First and most serious among them was the problem of maintaining, in such dry surroundings, a sufficient supply of water for protoplasmic activity. When the whole plant body is immersed in water, as is the case in primitive and lowly forms, an ample supply of this substance is always at hand. If a plant part is lifted up into the air, however, it at once is exposed to the danger of water loss through evaporation, which will soon result in death. If a plant is to succeed in such an arid environment it must be able both to absorb water in large amounts and to hinder the loss of water from its tissues by evaporation. Since the soil provides the only source of water available to a land plant, it is evident that *roots* or root-like structures must be developed to penetrate the soil and absorb water therefrom abundantly. A successful accomplishment of photosynthesis requires a large area of chlorophyll exposed to sunlight, and hence broad sheets of chlorophyll-bearing tissue, "waterproofed" to prevent undue evaporation, must also be evolved. These sheets are called *leaves.* The leaves cannot be too close together without depriving one another of the necessary light, and they therefore must be spread out and separated in some way on an axis or *stem.* The region where water is needed constantly to replace water loss may thus be far distant from the region where it is absorbed, and a well developed conducting system to carry water from root to leaf must therefore be differentiated in the stem tissues.

Aside from the difficulty of maintaining a sufficient supply of water, the land plant also faces problems of a mechanical nature. Owing to the buoyancy of water, a plant growing submersed therein needs little or no mechanical support. If it grows in the air, however, there is much weight to be carried and a heavy strain to be borne by the stem, especially in its lower portions. An extensive development of thick-walled skeletal and supporting tissue is thus necessary, especially in the stem, if the plant is to be kept firm and erect.

In order to be able to thrive on land a plant therefore must possess successfully functioning roots and leaves, and a stem able to serve as an efficient means of conduction and support.

Such structures are unknown in the thallophytes, and these plants therefore have never been able to invade the dry land and to produce a true terrestrial vegetation, although they often thrive in moist situations on land and may survive long periods of dryness in a dormant state. The first group to emerge from the water and develop land-inhabiting forms were probably the bryophytes or plants like them. They are developed best in moist places, though a few are aquatic and many grow in situations which are dry much of the time. Even in the most highly developed mosses, however, the root system is very weak and consists only of delicate thread-like rhizoids; the leaves are small and very thin, and the stems slender and with little or no development of supporting and conducting tissue. The mosses, therefore, do not grow more than a few centimeters high and have never succeeded in producing a strong and vigorous land vegetation.

It is a different matter with the pteridophytes, however. The dominant generation here is the sporophyte; and this new plant type, at least in all the forms which have survived to the present day, seems to be particularly well adapted to terrestrial life. Here for the first time occur true roots—large, vigorous, much-branched structures, each terminating in a mass of root hairs and well suited for rapid absorption and strong anchorage. The leaf is large and relatively thick, has a well-developed mesophyll of thin-walled cells, and is provided with abundant air spaces, the whole structure being covered by a stout epidermis to cut down evaporation. The necessary passage of gases between the outer air and the internal tissues of the leaf takes place through characteristic pores or *stomata*. The stem reaches a structural complexity nowhere exceeded among plants, the tissues for support and conduction being particularly well developed. The evolution of the true root, the true leaf, the stoma, and the highly differentiated stem made it possible for pteridophytes to produce the vigorous and abundant land vegetation which covered the earth in ancient times; and from this group have come the seed plants, which form the bulk of the terrestrial vegetation of today.

There is evidently a wide gap between the mosses on the one side and the ferns on the other. Transitional forms which must have existed between these two have entirely disappeared, and one can only guess what the plants were like which connected them, and what were the first steps in the evolution of the well-

developed land-inhabiting sporophytes which are so conspicuous today. This successful invasion of the dry land stands out as one of the most important and dramatic events in the history of the plant kingdom.

The Evolution of the Seed.—The last great progressive movement to be considered is the comparatively recent one (geologically speaking) which carried the process of reproduction to a still higher degree of efficiency and resulted in the development of that most perfect of reproductive structures, the *seed.*

The production of seeds is the distinctive feature of the spermatophytes or seed plants, which are now the most successful of all the higher plant types. The spore has several obvious disadvantages as a means of producing a new plant, owing to its minute size. Among the lower plants these difficulties are partially overcome by the production of spores in enormous quantities, but the system of independent, free-living gametophytes, developed from single-celled spores, is subject to many difficulties at best. In the seed plants, as in a few of the most advanced pteridophytes, there are two kinds of spores—*microspores* and *megaspores*—which produce male and female gametophytes, respectively. The happy innovation introduced by these highest plants was to retain the single megaspore within the spore case, intimately attached to the mother plant, where it germinates into a much reduced female gametophyte. This whole structure, with the addition of a coat or *integument,* is the *ovule.* Only a few ovules, in comparison with the great number of spores formerly produced, are borne by the plant. The microspores (pollen-grains) are still liberated into the air in great numbers, just as among lower plants; but instead of falling on the ground and germinating there, they are carried to the ovule or near it, where each produces two male gametes, one of which may fertilize the egg.

Not only have the seed plants abolished the delicate, free-living gametophytes, with all the consequent dangers and difficulties in the process of reproduction, but they have also established a much more successful method for insuring the growth of the young plant. The fertilized egg grows at once into the embryo, which draws the materials for its development directly and abundantly from the mother plant, and is thus relieved of the necessity of producing them by its own activity. About the embryo is deposited a supply of concentrated food in the endo-

sperm. The growth of the embryo ceases after a young root and one or two primitive leaves have been formed; and embryo and endosperm, tightly enclosed in the integument of the ovule which has become very tough and strong, is now the seed. This becomes detached from the parent plant and may remain in a dormant condition for a long time, sometimes many years; but on the occurrence of favorable conditions it will germinate and the embryo within it will begin to grow, bursting its shell, absorbing the stored food, sending forth roots and leaves, and rapidly developing into a new plant. The many advantages of reproduction by seeds over the old method of wind-blown spores and independent gametophytes are obvious, and it is easy to see why the seed plants have become so dominant and successful.

QUESTIONS FOR THOUGHT AND DISCUSSION

537. Why is it that new and distinct strains or races of corn, apples, or other plants which have been developed by breeders are not regarded as new *species?*

538. In the record of plant and animal evolution presented by fossils, why are there such large gaps?

539. What types of plants and animals would be most likely to be preserved as fossils?

540. Why is so little known about the evolutionary history of thallophytes from a study of fossils?

541. Aside from the evidence of fossils, what reason is there to believe that very many plant species formerly existed but have become extinct?

542. Characters which are apparently of the least functional importance to the plant are often most constant throughout large plant groups and are therefore very valuable in plant classification. Explain.

543. Most of the members of the Figwort family have four stamens in the flower, but there is often the rudiment of a fifth. The families nearly related to the Figworts all have five stamens. What inference may be drawn from these facts as to the evolution of the flower in the Figworts?

544. The plant population of an isolated island or island group in mid-ocean (such as the Hawaiian Islands) is composed very largely of

species which are found nowhere in the world except on that particular island or island group. Explain.

545. The potato, tomato, tobacco, and various other agricultural plants, now grown in Europe, are not native there but were introduced from America after the discovery of the New World. What conclusion can be drawn as to their evolutionary history?

546. *Torreya,* a genus of coniferous trees, is represented today by two species in China, one in California, and another in the southeastern United States, but is found nowhere else in the world. What conclusion can be drawn from these facts as to the past history of this genus?

547. In the Galapagos Islands very many of the plant *species* are confined to this group of islands, but most of the *genera* are the same as those found on the adjacent coast of South America. In Hawaii, it is not only the species which are distinctive of the islands but many of the genera are also found nowhere else. Which of these two island groups, on the basis of these facts, do you believe has been isolated the longer and the more effectively? Explain.

548. What two reasons can you suggest for the presence in a given region of local or *endemic* species (species found nowhere else)?

549. Plants living in arid or desert regions usually have small and leathery leaves and deep root systems, in contrast to plants living in regions of more abundant moisture. How would Lamarck explain this fact? How would Darwin?

550. Most species which are very common (abundant in individuals) belong to genera which are larger than the average in number of species. Explain.

551. Darwin noted that species belonging to large genera are usually more variable than species belonging to small genera. Explain.

552. Which is likely to be more successful, a relatively variable species or a relatively constant one? Explain.

553. Aquatic plants have in general relatively few species but these species have very wide geographical ranges. Explain.

554. Which might be expected to show more rapid evolutionary change, a plant species which is always cross fertilized or one which is always self fertilized? Explain.

555. State at least five advantages which one plant species might have over another which would make it more widespread and successful.

556. Give an example of a physical barrier to plant distribution; of a biological barrier.

557. Is competition generally keener between closely related, or between distantly related species, do you think? Explain.

558. In most cases, individual plants may be assigned to very definite species, and between these species transitional individuals are rarely or never found. If species have been developed through a gradual evolution, why are such transitional forms so rare?

559. A weed introduced into a new region often becomes more widespread and successful there than in its native land. Explain.

560. The chestnut-bark fungus, introduced some years ago into the United States, has exterminated all the native America chestnut trees over wide areas. In China, its native home, the species of chestnut are almost immune to attack. How do you explain this difference between American and Chinese chestnut species?

561. Some species of plants produce comparatively few seeds but are nevertheless just as successful as others which produce very many more. Explain.

562. During the glacial invasion the vegetation of the northern United States was obliged to migrate hundreds of miles south of its original range, and as the ice retreated it migrated northward again. What characteristics should a plant species possess to survive such a migration successfully?

563. Name at least five causes which might lead to the extinction of a species.

564. Why is it that all ancient and primitive types of plants have not been exterminated by the competition of those which have been more recently evolved?

565. A highly specialized and complex plant species is often less successful than one which is much simpler and more ancient in type. Compare, for example, the common bracken fern, which is relatively "low" in the plant kingdom but which thrives over almost the entire world, with many orchid species, which belong to one of the "highest" plant groups but are often rare and have very limited ranges. Explain these facts.

566. In the evolutionary history of many groups of plants and animals, as shown by their fossils, there is a gradual advance from simple and primitive members to those which are progressively more and more complex and abundant; but when a very high degree of specialization has arrived, the group suddenly disappears from the fossil record. Explain.

567. Primitive and ancient types of animals and plants are most common in comparatively isolated regions. Explain.

568. Do you think that evolutionary change will take place more rapidly in a region freely exposed to immigration from without, or in a comparatively isolated region? Explain.

569. The great land mass of Europe and Asia is believed to have been the center of evolution for many types of animals and plants now found in other parts of the world. Explain.

570. Do you think that the plant species with widest ranges are the oldest? Explain.

571. In consequence of the "struggle for existence" and the "survival of the fittest," why is it that in a given locality one species does not exterminate all the others and compose the entire vegetation?

572. Enumerate a few of the changes in the vegetation of the world which have been brought about by civilization.

573. Do you think that the first organisms to appear on earth were more like plants or like animals? Explain.

574. It is generally agreed that the earliest plants lived in the water. What evidence is there for this?

575. What are the advantages and disadvantages of a many-celled as compared with a single-celled plant?

576. What criteria may be used to determine whether a group of cells is a colony or a single plant individual?

577. Why is the increased size of the plant body, beyond a certain point, necessarily followed by the beginning of differentiation?

578. Why were the sexual cells probably among the first ones to be differentiated from the ordinary body cells of the plant?

579. In general, is there a higher degree of differentiation in the body of a water plant or of a land plant? Explain.

580. What other advantages are there, aside from increased vigor, which sexual reproduction may confer as compared with asexual?

581. In sexual reproduction, what is the advantage in having the two types of gametes (male and female) so radically different from one another?

582. Gametes, particularly male gametes, are often motile when all the other cells of the plant are not. Explain.

583. What various advantages and disadvantages can you suggest in the possession of an alternation of generations?

584. Why should it be that the alternation of generations, so well marked in lower plants, has practically disappeared in the highest ones?

585. Which were probably the first organisms to migrate from the sea to the land—plants or animals? Explain.

586. When the first plants invaded the dry land, with what kind of soil did they probably find it covered? What important changes did the presence of plants make in the soil?

587. Give a description of the probable appearance of the land surface before the evolution of the pteridophytes. What regions on earth today do you think it most closely resembled?

588. What effect did the evolution of the pteridophytes probably have on the abundance of land animals? Explain.

589. What similarities can you suggest between the evolutionary history of thallophytes, bryophytes, pteridophytes, and spermatophytes in the plant kingdom and that of fishes, amphibians, reptiles, and mammals in the animal kingdom?

590. What are the advantages of the seed over the spore as an agency of reproduction?

591. Why have seed plants largely superseded pteridophytes as the dominant element in the vegetation of the earth?

592. In what way has the evolution of seed plants probably changed the characteristics of plant-eating animals?

REFERENCE PROBLEMS

154. About how long do geologists estimate that life has existed on the earth?

155. What are the great geological periods into which the history of the earth has been divided by geologists? What is known as to the plant population of the earth in each period?

156. What are the earliest fossil plants known?

157. Describe the characteristics of one of the following extinct plant groups, state the geological period in which it chiefly flourished, and name the living plant group to which it is most closely related: the Calamites; the Lepidodendrids; the Bennettitales.

158. Give an example, not mentioned in the text, of a plant structure which seems to be vestigial.

159. What is meant by the statement that a given group of plants is (or is not) *polyphyletic?*

160. Give an example of the "recapitulation" of an ancestral trait in the developmental history of a plant.

161. What seems to have been the approximate place of origin of the following plants: orange, tobacco, squash, cocoanut, apple, Indian corn, cabbage, potato.

162. Summarize the life and work of Lamarck and state his important contributions to botany.

163. Summarize the life and work of de Vries and state his important contributions to botany.

164. Who was chiefly responsible for the establishment of our modern conception of the Alternation of Generations in plants?

165. Give the author and title of three important books dealing with evolution, and outline briefly the content of each.

166. Name several botanical investigators who have done important work in the field of plant evolution, and state the notable contributions made by each.

167. Give the derivation of the following terms and explain in what way each is appropriate:

Evolution	Zygote
Fossil	Sporophyte
Orthogenesi	Gametophyte
Gamete	Microspore

CHAPTER XIII

THE THALLOPHYTA

The simplest and most primitive members of the plant kingdom are the *Thallophyta* or thallophytes. This is a huge assemblage of species, about 80,000 in all, which display a wide variety in their structure and life histories. The name "thallus plants" refers to the character of their vegetative body, which is typically a *thallus,* or mass of tissue with little differentiation into such diverse organs as are found among the higher plants. It is usually rather small, and is often minute. This simplicity of their vegetative structures, together with their generally simple and primitive methods of reproduction, are the chief features which distinguish the thallophytes as a whole.

The group is by no means a homogeneous one and doubtless contains a considerable number of divergent lines of evolutionary ascent which have no very close relationship to one another. This diversity manifests itself in the size of the plant body, the degree of its differentiation, its physiological activities, its habitat, its methods of reproduction, and many other differences. The evolution of the multicellular plant body, the beginnings of vegetative differentiation, the origin of sex, the development of the saprophytic and the parasitic modes of life, and the first steps in the direction of an alternation of generations are among the important evolutionary events which have taken place in this immense and basal division of the plant kingdom.

In methods of reproduction thallophytes are particularly diverse. Asexual reproduction may be accomplished either by the division of an entire unicellular individual into two by *fission* or, much more commonly, by the formation of unicellular *spores* of various sorts. In aquatic forms these are usually motile, swimming about by means of cilia or similar organs, and are then known as *zoöspores.* In species living in the air they are various in form and origin, and are dispersed by the wind. Sexual reproduction is accomplished by the *conjugation* of similar gametes to form a *zygospore* or by the formation of dissimilar

gametes (male and female), which unite in *fertilization* to form an *oöspore.* In some of the fungi sexual union is followed by a rather complex process of spore formation.

To construct a truly natural classification for this heterogeneous group is a very difficult task indeed. The division as a whole is usually separated into two main series: the *Algae*, which possess chlorophyll or a similar substance and thus may live independently, and which include all the seaweeds, together with the pond scums and similar plants of fresh water; and the *Fungi*, which lack chlorophyll and therefore exist only as saprophytes or parasites, and to which belong the multitude of bacteria, molds, mildews, blights, rusts, toadstools, and mushrooms. The fungi have evidently arisen from several different groups of algae, so that the two series parallel one another somewhat in their various characteristics. It is more convenient to treat each separately, however, pointing out incidentally such relationships as seem clear between various groups in the two series.

THE ALGAE

The algae are usually divided into four chief classes: the Blue-green Algae, the Green Algae, the Brown Algae, and the Red Algae. There are also a number of minor groups the relationships of which are uncertain. The differences in color which have given rise to these names are incidental and are accompanied by more deeply seated morphological distinctions. Algae are primarily water plants, though a few inhabit moist situations on land. Many of the more minute species float freely, but the larger ones are usually attached to solid objects. The first two groups are common in both fresh water and salt, but the last two are confined almost entirely to the sea.

Cyanophyceae, or Blue-green Algae.—These are the simplest and lowliest of all green plants. The body consists of a single cell, but in most species these cells tend to adhere in colonies. The cell itself is very simple, lacking the nucleus, sap cavity, and chloroplasts so characteristic of other green plants. Its cytoplasm may be perfectly homogeneous, with the pigment evenly dispersed, or a colored outer zone and a colorless inner one may be roughly distinguishable. The latter perhaps represents a primitive nucleus. The pigment, which seems to be dissolved directly in the cytoplasm and never confined to definite plastids,

is usually (though not always) blue-green in color, and is probably a combination of chlorophyll with a blue pigment, *phycocyanin*. Both of these may be concerned with photosynthesis but this as yet is uncertain, for knowledge of the photosynthetic process in the blue-green algae is far less complete than it is for higher plants. It seems clear, however, that the product of photosynthesis is not glucose, as in ordinary plants, but glycogen, which is often found in fungi and which also constitutes the common storage carbohydrate in animals. The cell wall, which is described in recent investigations as consisting of pectic compounds with cellulose, is typically thick and mucilaginous; and in many species a group of cells becomes imbedded in the gelatinous mass derived from their walls so that a large, jelly-like colony results. On the occurrence of unfavorable conditions for growth, heavy-walled "resting cells" or spores may be produced. Cell division is very simple and shows none of the elaborate phenomena of mitosis, the cell merely becoming constricted by the growth of a new wall until complete separation into two cells has taken place. Little differentiation is evident, although peculiar large, dead cells frequently appear in certain species. Reproduction consists merely in cell division or fission, and no instances of sexuality have ever been observed in the class. In this respect the blue-greens differ from other algae but resemble bacteria, and these two groups have therefore sometimes been placed together as a separate division of the plant kingdom, the *Schizophyta* or Fission Plants, divided into the Schizophyceae (Cyanophyceae) and Schizomycetes (Bacteria).

The blue-green algae live in both salt and fresh water and are able to grow at higher temperatures than can any other plants, often thriving in the water of hot springs up to 60° C. Most species prefer water which is dirty and full of organic matter, and some may even be found on damp soil, rocks, and other situations which are exposed to the air.

One of the simplest examples is *Gloeocapsa* (Fig. 157, *B*), a minute, single-celled alga with a very gelatinous wall. As an individual divides, the resulting cells of the first generation, and usually those of the third and fourth, are held together, imbedded in their swollen cell walls. In *Oscillatoria* (Fig. 157, *A*) the cells are all alike and pressed flatly against one another in long filaments. The gelatinous wall is so poorly developed that these filaments are free in the water, where they sway or revolve

slowly. In *Nostoc* (Fig. 157, *C, D*) the cells occur in groups which are joined loosely into filaments somewhat resembling strings of beads. These may be imbedded in a jelly-like substance, the whole colony often reaching a diameter of a centimeter and containing hundreds of filaments. Here and there along the filament are found large, empty cells called *heterocysts.* Their function is not definitely known but in some cases they may be concerned in breaking up the filament into short segments, or

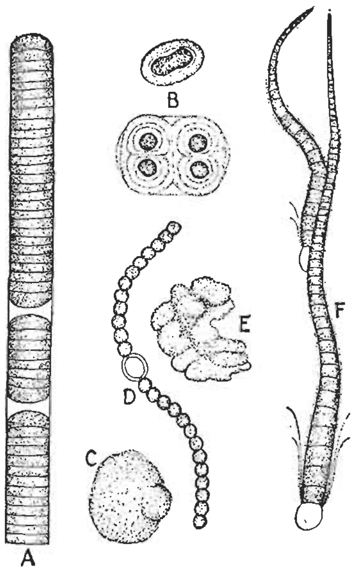


FIG. 157.—Cyanophyceae of various sorts. *A, Oscillatoria. B, Gloeocapsa. C, Nostoc* colony, natural size. *D*, filament of *Nostoc*, with a heterocyst in the middle of it. *E*, colony of *Rivularia*. *F*, filament of *Rivularia*, with heterocyst at base. (*E* and *F after Engler and Prantl.*)

hormogonia, which slip out of the enclosing wall and establish new colonies. Under certain conditions occasional cells may become greatly enlarged and thick-walled and are thus well adapted to survive unfavorable conditions. Some of the higher blue-green algae show branching, and in *Rivularia* (Fig. 157, *E,F*) the filament tapers to a finely pointed apex. It is often hard to decide whether the filament of a blue-green alga should be regarded as a colony of distinct individuals or as a single many-celled plant.

Chlorophyceae, or Green Algae.—This class is by far the largest of the four groups of algae and its members are very

diverse. They contain chlorophyll and its associated carotin and xanthophyll, but usually no other conspicuous pigments, and the bright green color which the plant body thus displays has given the class its name. It is well represented in both fresh and salt water and a few species thrive in damp situations on land. The cell is much more highly differentiated here than among the blue-green algae, possessing a nucleus, one or more chloroplasts (often called *chromatophores*), and usually a sap cavity, thus resembling in its essential details the cells of the higher plants. *Pyrenoids*, or centers of starch formation, are prominent in the chloroplasts. The plant body may consist of a single cell, a colony, a filament, or a plate of cells. Most species (though not all) produce *zoöspores*, motile reproductive cells which swim about by the aid of one or more lashes or *cilia*, and which grow directly into new plants. These are developed in modified cells or *sporangia*. Various types of sexual reproduction are also found in this class, ranging from instances where the gametes are entirely similar to those where they have become markedly distinguishable as *sperms* and *eggs*. Because of all this structural diversity and of the fact that they are thought to be near the main line of ascent from lower algae to bryophytes, the Chlorophyceae have received intensive study, particularly with regard to the development of the multicellular individual and the evolution of sex.

This great class has been divided into a number of more or less homogeneous groups, though the relation of these to each other is not always well understood. The characteristics of each of these groups may be presented most clearly by describing several typical members of each.

The One-celled and Colonial Green Algae (*Volvocales*).—These are chiefly microscopic plants, and the individuals are single-celled, although they are often loosely joined into colonies. Many of the forms are able to move about actively by means of minute, thread-like cilia.

Carteria (Fig. 158) is typical of the more primitive members of the order in being a free-swimming form. Inside the delicate but firm cell wall the space is nearly filled with a single massive chromatophore (chloroplast), somewhat like a thick-bottomed cup in form; the hollow of this structure is filled with colorless cytoplasm in which the nucleus lies. From a point at the top of this colorless portion four delicate protoplasmic threads, the cilia, extend out through the cell wall. At their base are two

contractile vacuoles, which pulsate rhythmically in alternation, discharging their contents often at intervals of fifteen seconds. A pyrenoid, often showing a sheath of starch grains, lies in the basal part of the chromatophore, and the red pigment spot (often called the "eye-spot"), toward the anterior end. Either while the cell is still actively swimming or after the retraction of the cilia, the protoplast may divide into two or four daughter cells, which secrete new walls and develop their own cilia before they escape by breaking through the wall of the mother cell. These daughter cells, or zoöspores, soon grow to the normal size.

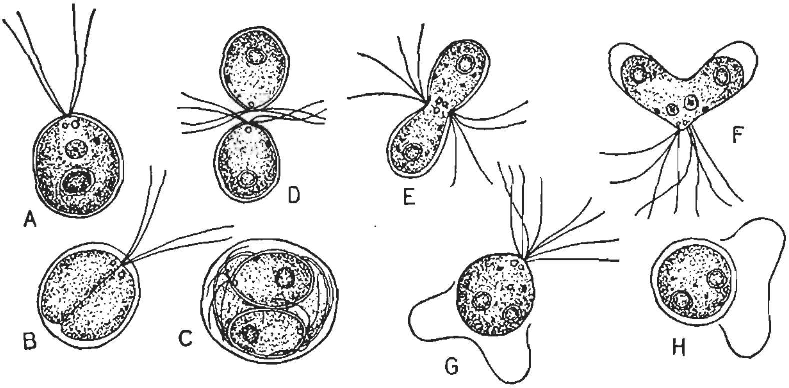


FIG. 158.—*Carteria.* *A*, vegetative cell, showing massive chromatophore, contractile vacuoles, eye spot, nucleus, and pyrenoid; *B*, beginning of cell division; C, four daughter cells developed within the mother cell wall; *D*, gametes; *E-G*, conjugation; *F*, gamete protoplasts slipping out of their walls; *G*, fusion completed, motile zygote free from gamete walls; *H*, thick wall developed about the resting zygospore. (*A-D after Hazen. E-H after Goroschankin.*)

Under certain conditions, smaller, but otherwise similar motile cells are formed, usually by the division of the mother cell into eight, and these, after a brief period of very active motility, unite in pairs. These are the *gametes*, and in this case their evolution from ordinary zoöspores or vegetative cells is very clear. The cell formed by their union continues active locomotion for a time (sooner or later throwing off the gamete walls), showing two eyespots, two pyrenoids, and two nuclei. Presently it comes to rest, draws in its eight cilia, the two nuclei fuse, and a new thick wall is secreted about this zygospore. Such a form of sexual reproduction is known as *isogamy*. *Carteria* may be regarded as a fundamental form, for there are many genera among the higher

green algae which produce 4-ciliate zoöspores very similar in character to the vegetative cells here.

Carteria is undoubtedly derived from simpler forms which might be placed among the Flagellates, a series of somewhat diverse groups possessing plant-like and animal-like characteristics, which have probably given rise to lines of development in both kingdoms. These flagellate ancestors differ from *Carteria* chiefly in the lack of a definite cell wall, the cell being bounded only by a delicate protoplasmic membrane.

Chlamydomonas (Fig. 159), much more common and better known than *Carteria*, has cells of entirely similar character except

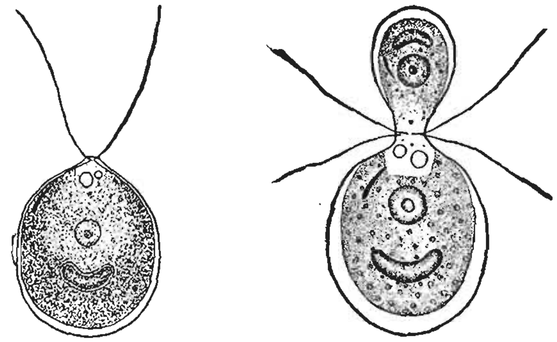


FIG. 159.—*Chlamydomonas*. *A*, individual plant, showing the two contractile vacuoles under the base of the cilia, the central nucleus, the "eye spot," and the crescent-shaped pyrenoid imbedded in the massive chromatophore. *B*, union of two gametes. In most instances these gametes are equal in size but in the case figured they are distinctly different. (*After Goroschankin.*)

that the cilia are reduced in number to two. Many more species are known in this genus, and some of them show interesting variations in their reproduction. Most of them are isogamous; but the one illustrated, for example, has gametes of unequal size, a larger one regularly conjugating with a smaller one. Such a differentiation of size in so primitive a form is surprising, for it anticipates the condition leading up to the complete differentiation of sperm and egg cells, which is more often associated with higher types.

There are a number of other algae with cells similar to *Chlamydomonas* except that they are united into loose colonies of ciliated individuals, and the group culminates in the large, hollow, spherical colonies of *Volvox* (Fig. 160) which often consist of

thousands of cells. In these higher forms the sperms are markedly different from the eggs, and the cell formed by their union is thus a fertilized egg or oöspore (Fig. 160, *C*). Sexual reproduction of this type is known as *heterogamy*. It should be noted that

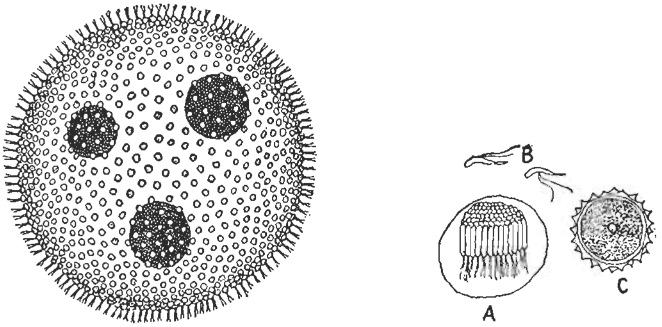


FIG. 160.—*Volvox* At left, globular colony of biciliate individuals, with three daughter-colonies developing in its interior. At right, sexual reproduction. *A*, group of sperms developed within a single cell; *B*, sperms; *C*, fertilized egg or oöspore. (*A-C after Cohn.*)

both zygospores and oöspores are typically thick-walled cells which are capable of resisting such unfavorable conditions as drought and low temperature, and of germinating to produce new plants whenever a suitable environment again appears.

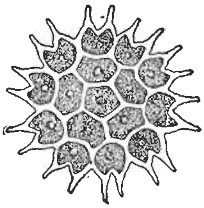


FIG. 161.—*Pediastrum.* A group of sixteen cells united into a plate-like colony.

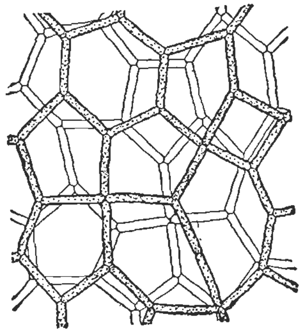


FIG. 162.—*Hydrodictyon.* Portion oı a net-like colony, individual cells forming the meshes of the net.

In another family of Volvocales the body cells are non-motile, independent movement being limited here to the zoöspores and the gametes. The individuals are united in colonies which are simple, few-celled plates in *Pediastrum* (Fig. 161) but form a complex network in the water-net, *Hydrodictyon* (Fig. 162).

The zoöspores do not escape from the mother plant and swim about, as is usually the case, but the group of zoöspores formed within a single mother-cell displays the remarkable habit of uniting, while still within this cell, to form a minute colony of non-motile cells which is finally liberated and grows into a mature colony.

The Volvocales are of especial importance because of the light which they throw upon the development of the multicellular individual and the differentiation of the sexes.

Filamentous Algae (*Ulotrichales*).—In this group the cells of the vegetative body are either attached end-to-end to form a thread or filament or, by divisions in all directions but within the same plane, form a delicate membrane. Most of the common filamentous and membranous green algae of both salt and fresh water belong here. They all reproduce asexually by zoöspores, but exhibit various types of sexual reproduction. The order is large and varied and many of the species within it are but distantly related to one another. A description of three typical members will present some of the important characters of the group.

Ulothrix (Fig. 163) is a common thread-like alga, its short cells each containing a single nucleus and a large, girdle-shaped chloroplast. It is found in rather cool water and each filament is attached to a rock or other solid object (its *substratum*) by a basal cell, which is narrow, elongate, and generally lacking in chlorophyll, and is known as a *holdfast*. The development of this cell, so different from those which form the rest of the filament, is an example of the beginning of that process of division of labor, or *differentiation*, which is so pronounced in more complex plant bodies.

Under certain conditions the contents of any cell (except the holdfast) may divide into a group of naked zoöspores, usually 2, 4, 8, or 16 in number, which escape through a small opening in the side of the cell. Each zoöspore has four cilia and swims about actively for a time, but finally settles down on some solid object, elongates, and by transverse division, repeated in the daughter cells, develops into a new filament. These zoöspores closely resemble individuals of *Carteria*.

Other cells of the filament may divide into somewhat smaller motile cells which have two cilia instead of four, but are otherwise hard to distinguish from zoöspores. These are the gametes, and ultimately they unite (or *conjugate*) in pairs to form a zygospore,

the contents of which after a time forms a group of non-motile spores or of zoöspores. Each of these may grow into a new filament.

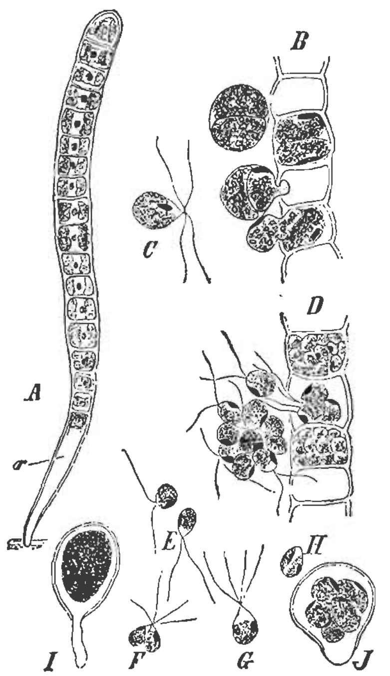


FIG. 163.

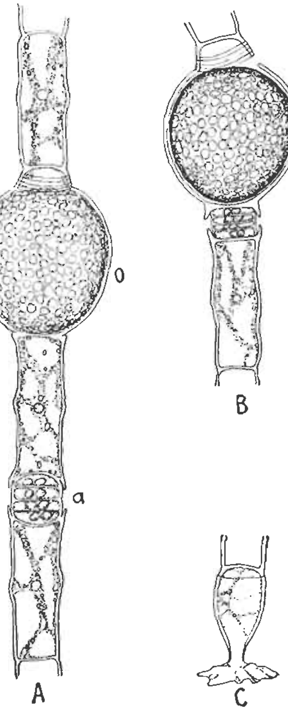


FIG. 164.

FIG. 163.—*Ulothrix*. *A*, young filament with rhizoid cell (*r*) by which it is attached; *B*, portion of filament with escaping zoöspores; *C*, single zoöspore; *D*, formation and escape of gametes; *E*, gametes; *F* and *G*, stage in the conjugation of two gametes; *H*, zygote or zygospore; *I*, zygote beginning to germinate; *J*, group of zoöspores produced by a zygote. (*From Strasburger, after Dodel-Port.*)

FIG. 164.—*Oedogonium nodulosum*. *A*, filament with antheridium (*a*), each cell of which produces two sperms; and oögonium (*o*), containing one large egg; *B*, filament with a thick-walled oöspore (*os*) which has developed from a fertilized egg; *C*, basal cell of a filament, showing holdfast.

Oedogonium (Fig. 164) is another common filamentous form. It is anchored by a more complex holdfast than that of *Ulothrix*, and its cells are more elongated and have a specialized mode of division. Each has a single large, reticulate chloroplast in the form of a hollow cylinder. In certain cells the entire cell contents may round up into a single large zoöspore, with a circle of cilia

near one end. This escapes and swims about for a time but soon attaches itself and grows into a new filament.

In its sexual reproduction *Oedogonium* shows a marked advance over *Ulothrix* in the fact that its gametes, like those of *Volvox*, are of two sorts. Certain cells become much enlarged and each produces a single rounded, non-ciliated cell, well supplied with chloroplasts and food material. This is the female gamete or *egg*, and the cell which produces it (like all egg-producing structures in these lower plants) is called an *oögonium*. In other cells, the

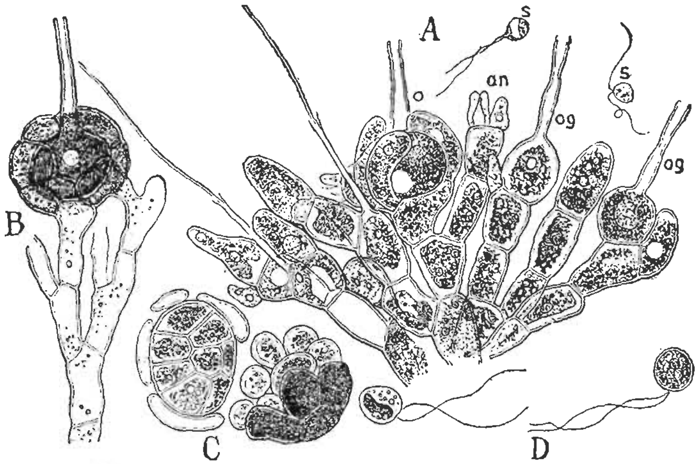


FIG. 165.—*Coleochaete*. *A*, portion of fertile thallus. *og*, oögonium, containing a single large egg. *an*, antheridium. *s*, sperm. o, oöspore or fertilized egg, which is beginning to be surrounded by filaments growing up from below. *B*, mature fructification, the oöspore surrounded by an envelope of cells. *C*, the contents of the fructification dividing up into zoöspores. *D*, zoöspores. (*From Goebel, after Pringsheim.*)

contents divide into two small, motile male gametes or *sperms*, and each of these sperm-producing cells (like all structures which produce male gametes) is known as an *antheridium*. One of the sperms enters an egg and fertilizes it, and the oöspore thus formed becomes very thick walled. Eventually it is liberated and after a period of dormancy germinates into a group of four zoöspores, each of which grows into a filament. Because of the peculiar character of its zoöspores and sperms (both being provided with a crown of cilia) *Oedogonium* is often placed in a separate order.

Coleochaete (Fig. 165) is a fresh-water alga the vegetative body of which consists of a flat plate or cushion of radiating filaments. Its cells may produce single, large, biciliate zoöspores. Antheri-

dia and oögonia are formed much as in *Oedogonium*, and a thick-walled oöspore is produced. Following this, however, the adjacent cells give rise to branches which grow up and surround the oöspore, forming a distinct spore case or fruiting body. The oöspore germinates into a group of cells each of which ultimately forms a zoöspore which grows into a new plant. This type of reproductive cycle is one of a series of characters in the algae which are regarded as foreshadowing the typical alternation of generations of higher plants. In its structure and life history *Coleochaete* is one of the most specialized of the green algae and has been regarded by many botanists as approaching somewhat closely the lowest bryophytes.

FIG. 166.—*Pleurococcus*. Single cell and two small groups of cells.

Pleurococcus (Fig. 166), which forms the green coating on damp bark, rocks, and similar places, is one of the commonest and most widely distributed of green algae. The cell contains one large, plate-like chromatophore. It has apparently lost the power of producing zoöspores and gametes, and multiplies through cell division, which is of the type found in *Ulothrix*. The daughter cells usually remain united for a time in small groups (or even short filaments), but ultimately separate. This is often treated as a one-celled type among the Volvocales, but its structure and method of division have led to its being regarded in modern schemes of evolutionary classification as a reduced member of the Ulotrichales. This or similar algae are often associated with a fungus to form the composite thallus of certain members of that peculiar group, the *lichens* (Fig. 203).

Tubular Algae (*Siphonales*).—These are distinguished from all other algae by the fact that the whole plant body, whether it be a simple filament or a well differentiated thallus, is essentially a *single cell.* The cross walls which divide the plant body of most other algae and of all ordinary plants into small cells are absent, and the mass of cytoplasm with its thousands of nuclei is therefore able to circulate freely throughout the whole plant. Such a multinucleate cell, of which these plants are extreme examples, is known as a *coenocyte.*

The Siphonales are chiefly marine forms, especially abundant in the warmer seas. They normally form zoöspores, and in cases

where sexuality has been proved usually produce two motile gametes of unequal size except in the genus *Vaucheria*, which is such a familiar and distinctive type that it is studied very commonly. This alga forms the common "green felt" so often

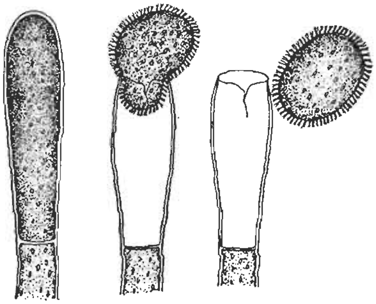


FIG. 167.—*Vaucheria.* Asexual reproduction. The tip of a filament is cut off by a wall and its contents becomes a large zoöspore, with many nuclei and many groups of paired cilia. The zoöspore breaks through the wall and escapes. (*After Gotz.*)

found on damp soil or in muddy pools, and consists of a tangled mass of coarse, branching, tubular filaments. This plant is different from most algae in the fact that pyrenoids or centers of starch formation are absent from its chloroplasts, and that oil

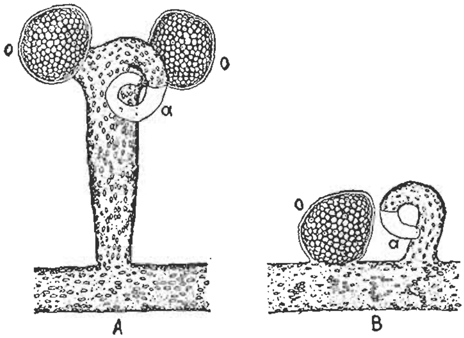


FIG. 168.—*Vaucheria.* Sexual reproduction. Oögonia, *o*, each contain a single egg. Antheridia, *a*, have discharged all their sperms and are empty. *A*, *V. terrestris.* *B*, *V. sessilis.*

rather than starch is the type of reserve food. Large multinucleate zoöspores are produced, each of which is merely the contents of the tip of a filament which has been cut off by a wall and has escaped (Fig. 167). The sexual organs are not merely modified vegetative cells, as in the plants previously studied, but

are specialized for gamete production (Fig. 168). A cell partitioned off by a wall from the main filament or from a small lateral branch becomes the oögonium, within which a single large egg is formed. From the tip of another small branch near by is cut off a cell which develops into an antheridium. The uninucleate sperms here formed enter the oögonium and one of them fertilizes the egg, producing a heavy-walled oöspore. After a dormant period this germinates directly into a new filament.

Pond Scums and Desmids (*Conjugales*).—The plant body of these algae is a single cell or an unbranched filament. The species are all confined to fresh water and are distinguished from other Chlorophyceae by the absence of zoöspores or other means of asexual reproduction, the absence of motile cells of any sort, the occurrence of large and conspicuous chromatophores, and the characteristic manner in which sexual reproduction is brought about.

The Pond Scums, of which *Spirogyra* (Fig. 169) is the common example, are all filamentous algae. In this genus the chromatophore is a broad, strap-shaped structure running spirally around the cell, and on it appear a series of small, rounded areas, the pyrenoids. The nucleus is suspended in the middle of the sap cavity by threads of cytoplasm extending to the walls. In sexual reproduction, adjacent cells of two filaments which are lying side by side send out projections or *conjugating tubes* toward one another. The tips of these touch, the wall between them breaks down, and through the channel thus formed the whole protoplasmic contents of one cell enters the other and the living portions of the two cells fuse into a thick-walled resting zygospore. Occasionally the two cells conjugate in the tube itself, and sometimes two adjacent cells of the same filament may unite.

The *Desmids* (Fig. 170) are unicellular plants of the utmost variety and beauty of form, and are often ornamented by spines, protuberances, and markings of various sorts. The cell is composed of two perfectly symmetrical halves separated by a zone, the *isthmus*, which is often constricted and under which lies the nucleus. Aside from ordinary cell division, reproduction is effected by conjugation between two protoplasts, each of which has escaped from its wall. Some of the simpler desmids show a considerable resemblance to *Chlamydomonas* in their mode of conjugation and in the germination of the zygospore. From these simpler desmids there are evidences of a progressive upward

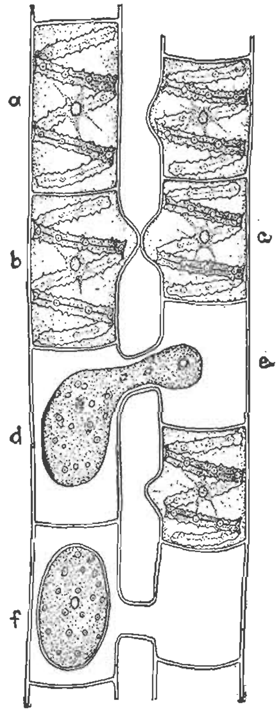


FIG. 169.—*Spirogyra*. Two adjacent filaments, showing stages in sexual reproduction. Cell *a* shows the normal, resting condition, with the spirally placed, band-like chromatophore, in which numerous circular pyrenoids can be seen. Cells *b* and *c* are sending out conjugating tubes to each other. The contents of cells *d* and *e* have contracted somewhat and the contents of *e* is passing over through the conjugating tube and uniting with *d*. At *f* is shown the mature zygospore which has arisen from the union of two cells.

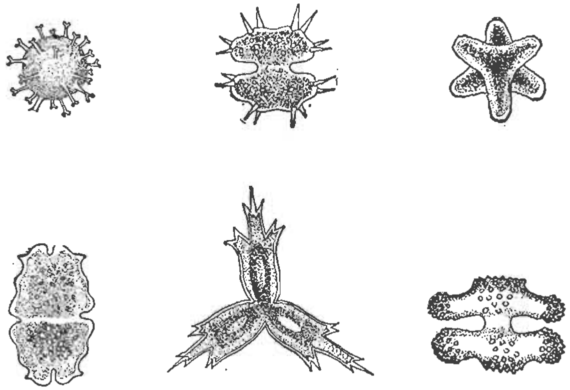


FIG. 170.—Desmids of various types.

development to the more specialized conditions found in *Spirogyra* and related filamentous forms.

Stoneworts (Chara and Nitella).—This remarkable class of plants (Fig. 171), though like the Chlorophyceae in its pure green

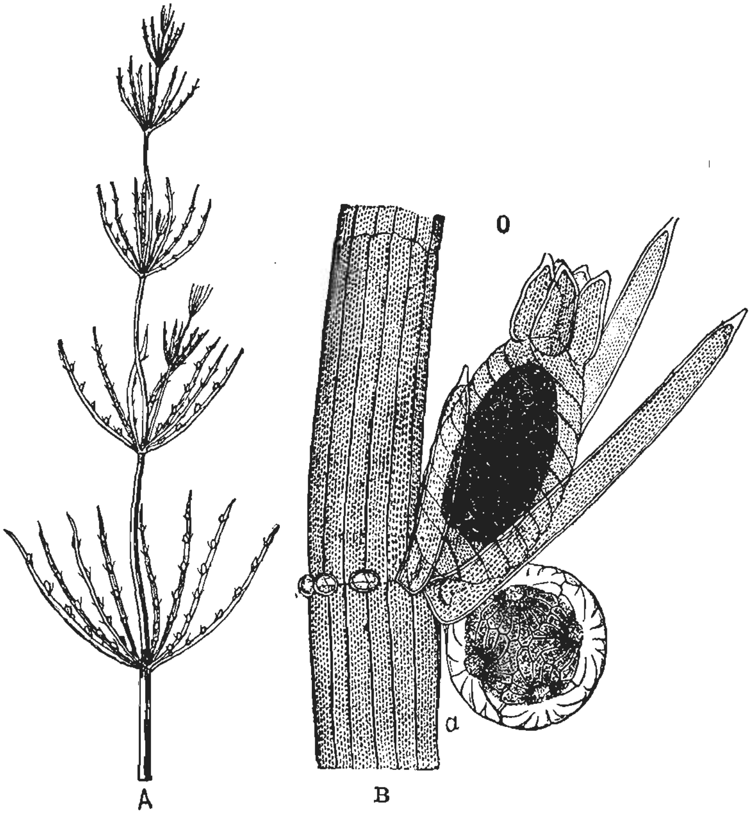


FIG. 171.—*Chara*. *A*, a main branch, showing the circles of small, lateral branches, bearing the sexual organs, arising at the joints of the main branch. *B*, a portion of a branch, showing the main axis and the short side branches, near the union of which are attached an antheridium (*a*) and an oögonium (*o*). (*B after Sachs.*)

color, stands apart from all others in its morphology and there is no certain knowledge as to its relationships. The vegetative body consists of long, jointed stems, and at the joints, or nodes, arise whorls of short branches. No asexual spores are produced but along the branches are borne antheridia and oögonia, far

more complicated than among any other thallophytes. The antheridium is spherical and its wall is composed of eight somewhat triangular cells from the inner surface of which arise a large number of many-celled, sperm-producing filaments. The oögonium is covered with a wall or envelope of spirally wound cells growing up from the tissue below it, and produces a single large egg. After fertilization the envelope hardens, forming a nut-like spore case around the oöspore. The absence of anything suggesting an alternation of generations indicates that these plants should be placed among the thallophytes, but they are clearly distinct from any other members of the division.

Phaeophyceae, or Brown Algae.—These plants may be distinguished from other algae by their characteristic brown color, due to one or more brown pigments associated with chlorophyll, and by certain structural characters. The Phaeophyceae are the largest and rankest of all algae and display the highest degree of bodily differentiation. None of them are unicellular. They are found almost exclusively in the sea, and are best developed in the cooler regions. Thriving most commonly in shallow water and the zone between tide marks, they are subjected to the buffeting of the waves and may be exposed to the air for several hours a day. These plants probably represent an entirely independent line of evolution from the green algae or from flagellates, and seem to have led to no higher types. The three most important orders among them are the *Ectocarpales*, *Laminariales*, and *Fucales*.

Ectocarpales.—*Ectocarpus* (Fig. 172), one of the best-known genera, is a rather small, filamentous plant. As in the algae previously studied, the zoöspores are produced here in sporangia which are modified single cells. The gametes, however, are developed in large multicellular structures (*plurilocular* sporangia) which begin to show a resemblance to the highly developed sexual organs characteristic of the bryophytes, and are not usually borne on the plants which produce zoöspores. Each of the many small cells into which the contents of this structure is divided forms one or two gametes, which after swimming about fuse in pairs to produce zygospores. Instances have been reported in which these gametes germinate directly into a new plant, and thus function essentially like zoöspores, which they much resemble structurally. Gametes of different size and state of motility sometimes unite, thus indicating the beginning of a

heterogamous condition. Types like *Ectocarpus* seem to display the beginning of the differentiation of sex in the brown algae.

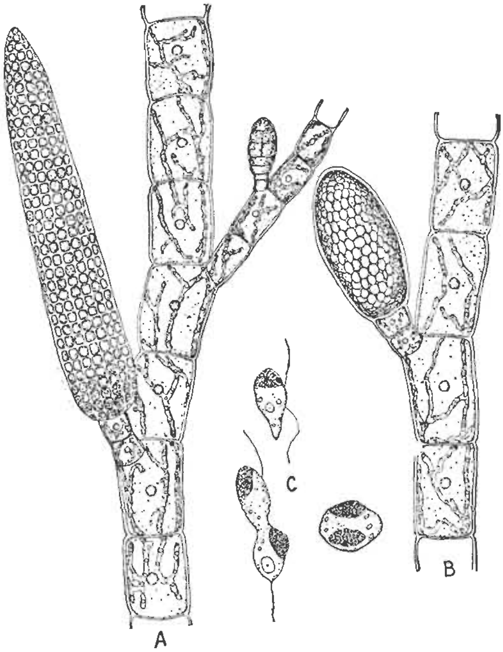


FIG. 172.—*Ectocarpus*. *A*, filament with multicellular or plurilocular sporangia, in which gametes are produced. A young and growing sporangium is shown above. *B*, filament with a single-celled sporangium, in which zoöspores are produced. *C*, various stages in the union of two gametes. Above, a single gamete; at left, the beginning of union; at right, the resulting zygospore. (*C after Oltmanns.*)

Kelps (Laminariales).—In this order occur the kelps (*Laminaria*) common in the north Atlantic and elsewhere, together with many other large algae such as the giant kelp (*Macrocystis*), the sea-otter's cabbage (*Nereocystis*), the sea palm (*Postelsia*), and other smaller types. The larger kelps may become huge plants, sometimes perhaps attaining a length of one hundred meters. They are attached to the rocks by massive holdfasts. The stout "stems" or *stipes* support broad and frequently much-divided blades and often display a considerable degree of structural differentiation.

In *Laminaria* itself, the commonest of the kelps, it has been shown that the abundant zoöspores do not grow directly into

individuals similar to those by which they were produced, but instead germinate into minute sexual plants, very different from the kelp, some of which bear antheridia and produce sperms, and others oögonia and eggs. From the fertilization of an egg by a

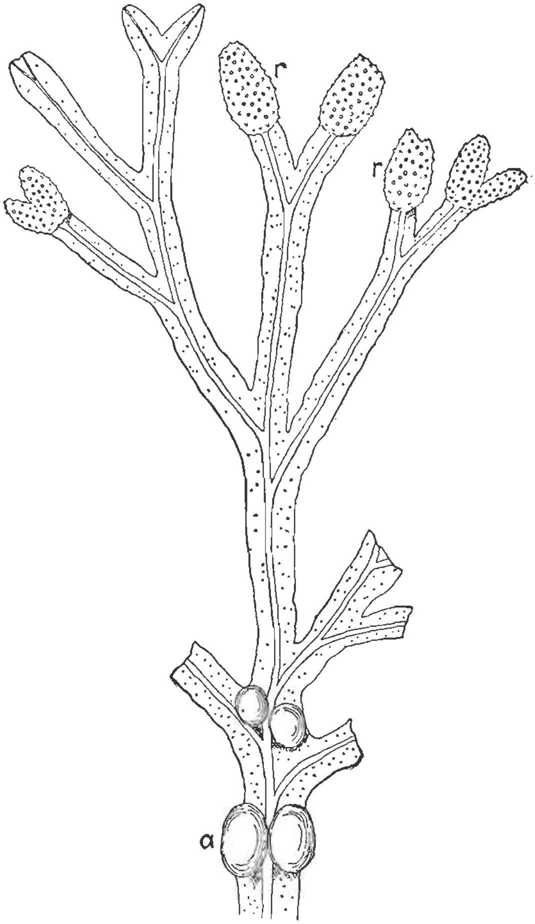


FIG. 173.—*Fucus vesiculosus.* Portion of thallus showing air-bladders (*a*) and receptacles (*r*). On the surface of the latter are the many small openings of the conceptacles.

sperm there is developed a typical kelp plant, which again bears zoöspores. *Laminaria* thus exhibits a typical alternation of generations like that of the higher plants, a non-sexual plant producing spores which form sexual plants, from which the non-

sexual plant again develops. Such a life history may be more common among brown algae than was formerly supposed.

Rockweeds (*Fucales*).—These plants differ from the kelps in producing no zoöspores and in displaying no evident alternation of generations.

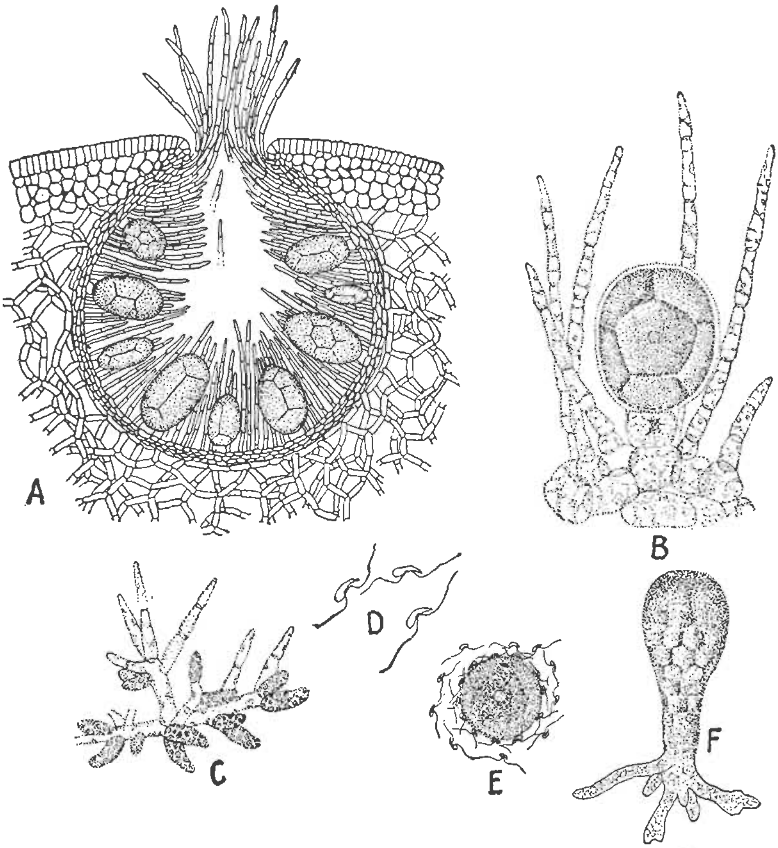


FIG. 174.—*Fucus*. *A*, female conceptacle, with oögonia and sterile filaments. *B*, single oögonium at maturity, containing eight eggs. *C*, group of antheridia from a male conceptacle. *D*, sperms. *E*, egg after discharge into the water, surrounded by sperms. *F*, young plant arising from an oöspore. (*B*, *C*, *D*, *E* and *F* after *Thuret*.)

Fucus, the best known genus, is exceedingly abundant on rocks between tide marks in the temperate regions. The vegetative body of this alga is a flat, repeatedly forking, ribbon-like thallus usually provided with air bladders (Fig. 173). It elongates by the activity of definite growing regions at the ends of the free

branches, the center of each growing region being occupied by a single actively dividing *apical cell.* The swollen tips of certain branches are known as *receptacles* and bear the sexual organs. Scattered over these tips, just below the surface, are many small chambers or *conceptacles*, each opening to the outside by a pore. Lining the wall of these chambers are masses of branching filaments or *paraphyses*, among which are borne the antheridia and oögonia (Fig. 174). The antheridia are small cells arising on branches of the filaments and producing swarms of biciliate sperms. The oögonia are larger cells, the contents of each dividing into eight eggs. In some species both sex organs are produced in the same conceptacle, in others they occur in different conceptacles on the same plant, and in still others the whole plant is entirely male or entirely female. Both eggs and sperms are discharged from the mouth of the conceptacle and fertilization takes place in the open water outside. The oöspore settles to the bottom, attaches itself, and develops directly into a new plant.

The Diatoms.—Similar to the brown algae in color but distinct in many respects are the diatoms, a large group of unicellular algae found very commonly both in fresh and salt water (Fig. 175). They are the most abundant of the minute plants which make up that multitude of freely swimming or floating algae known as the *plankton.* Many species are also sessile and may be united into filaments or other colonies. The wall is hard and flinty, being heavily impregnated with silica, and consists of two halves or *valves*, one of which fits over the other like a box cover. These are very diverse in shape and are often ornamented with minute and intricate markings which long have been the delight of microscopists. Each cell ordinarily contains two chromatophores which possess a brown pigment masking the chlorophyll. The cell divides into two by fission, each half carrying with it one of the valves of the original cell and regenerating one new one. This method of division results in a decrease in cell size. Occasionally the contents of two cells escape from their walls, increase in size, and unite to form a zygote which in turn develops into a full-sized individual.

Rhodophyceae, or Red Algae.—These are a very varied group, rich in species, almost exclusively marine, and reaching their best development in the warmer seas. Most of them grow entirely submersed, below tide marks, and are therefore not particularly conspicuous or familiar. The vegetative body tends to be deli-

cate, filamentous, and much-branched, in contrast to the bulky thallus of the brown algae. The cell wall is often thick and gelatinous and the cells thus give the appearance of being imbedded in jelly. In most forms, also, there is a definite cytoplasmic connection between each cell and the adjacent members of the same filament. The Rhodophyceae are distinguished from

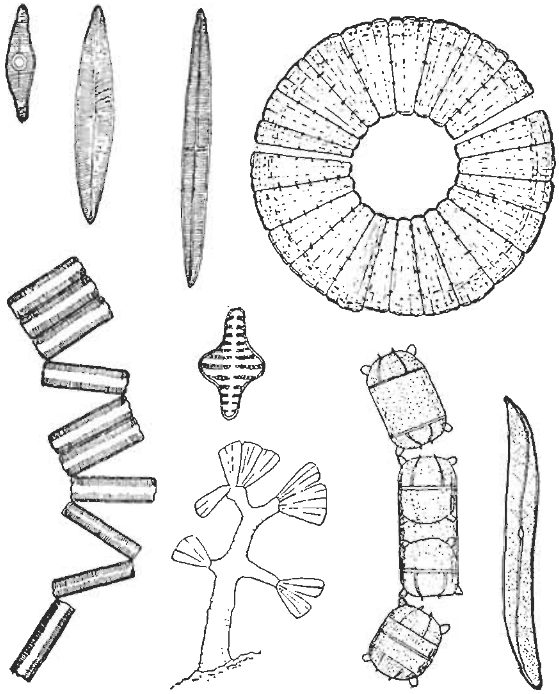


FIG. 175.—Diatoms of various types.

all other algae by their characteristic reddish color (due to the pigment *phycoerythrin* which is present with chlorophyll), by the complete absence of motile cells of any kind, and by a highly specialized type of sexual reproduction. They do not include primitive types but seem to have arisen from a point already well up in the scale of algal evolution. The higher members of the class display an unquestionable alternation of generations. Two typical genera will illustrate the complexities of reproduction in this group.

Nemalion (Fig. 176) is a common form with a branching, filamentous habit and is representative of the simpler red algae. The numerous small antheridia produce non-motile sperms. The female sexual apparatus, which is here called the *procarp*, is a short, specialized branch whose terminal flask-shaped cell consists of a swollen basal portion, the *carpogonium*, containing the

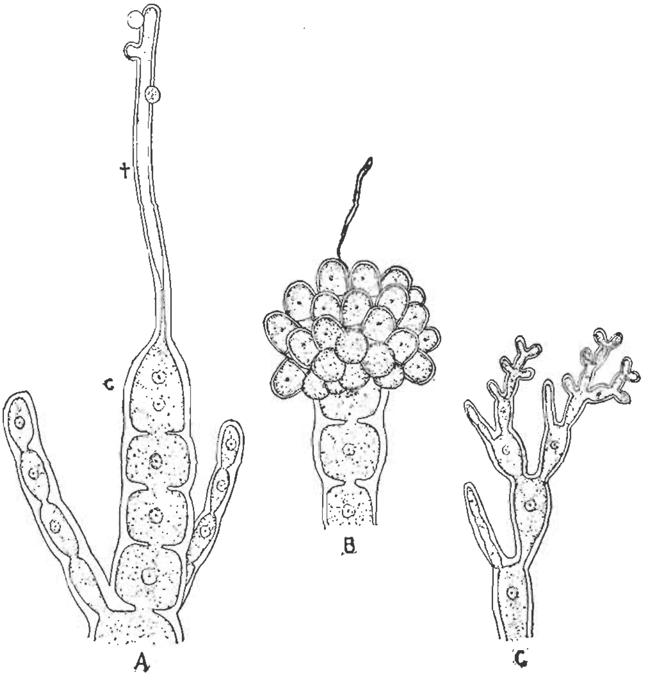


FIG. 176.—*Nemalion*. *A*, procarp at end of a filament. *c*, carpogonium and *t*, trichogyne, to which several sperms are attached. A male nucleus has entered the carpogonium. *B*, cystocarp, which has arisen from the fertilized carpogonium. Carpospores are developing at the ends of short filaments. *C*, antheridia, groups of small cells each of which produces a sperm.

single egg cell and homologous with the oögonium of green algae. This is prolonged upward into a hair-like extension, the *trichogyne*. The sperm is carried by water currents to the trichogyne, down which its contents passes into the carpogonium. The fertilized carpogonium does not develop a new plant directly, but produces a group of short, branched filaments on the end of each of which is borne a non-motile *carpospore*. This whole structure of spores, filaments, and carpogonium is known as the *cystocarp*. A carpospore germinates directly into a new plant.

Polysiphonia (Fig. 177) is another common member of the class, and has a much-branched thallus consisting of a central core surrounded by a jacket of filaments. It displays a much more complex sexual history and is typical of the majority of the red algae. Three types of plants, similar in vegetative structure but differing in their reproductive organs, may be distinguished: male plants, producing antheridia only; female plants, producing procarps only; and sexless *tetrasporic* plants, producing sporangia in each of which are four asexual *tetraspores*. The procarp is

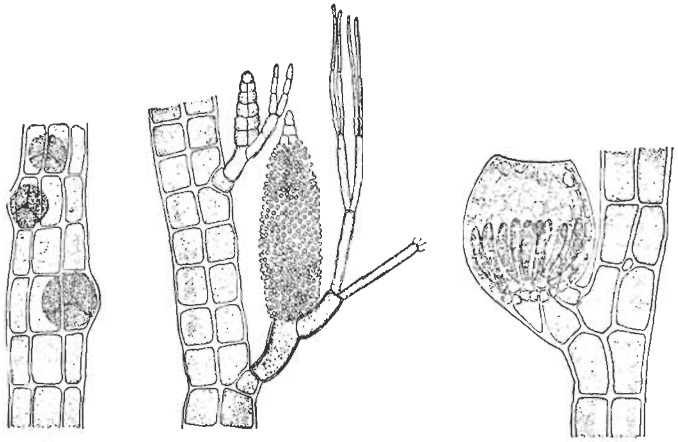


FIG. 177.—*Polysiphonia fibrillosa*. *A*, portion of a tetrasporic plant showing three groups of tetraspores. These spores occur in *tetrads* or groups of four. *B*, portion of a male plant. Above, an immature antheridium; below, a mature one, producing large numbers of sperms on its surface. *C*, portion of a female plant showing a ripe cystocarp, its wall enclosing a group of carpospores.

somewhat more complex than in *Nemalion* since it contains a group of *auxiliary cells*. Fertilization, however, occurs in much the same way, a sperm coming in contact with the trichogyne, entering the carpogonium, and fusing with the female nucleus. Some rather complicated fusions now take place between the fertilized carpogonium and the auxiliary cells, as a result of which sixty or more carpospores are produced. An envelope of sterile cells grows up from the base and encloses this spore mass, forming the cystocarp.

Experiment has established the fact that these carpospores produce only tetrasporic plants, and that the tetraspores in turn produce only male or female plants. Thus a regular alternation

of sexual and non-sexual individuals is set up. Cytological examination has proved further that the tetrasporic plants have twice the number of chromosomes possessed by the sexual plants, and there seems no reason to doubt that there is here a true alternation of generations, the tetrasporic plant (plus the cystocarp) constituting a sporophyte, and the sexual plants, gametophytes. This is the more remarkable since all the plants are perfectly similar in their vegetative structures.

The red algae are very evidently a specialized class and although they have reached a marked degree of complexity, they apparently have not been the ancestors of anything higher up in the evolutionary series among chlorophyll-bearing plants. They are generally regarded, however, as having given rise to some of the higher fungi by the assumption of a saprophytic or parasitic habit with the accompanying or consequent loss of chlorophyll.

THE FUNGI

The other great group of the thallophytes are the fungi, which are distinguished from algae by the absence of chlorophyll. Their consequent inability to manufacture food therefore compels fungi to live either as saprophytes or as parasites. Like the algae this is a heterogeneous group, and many of its members seem more closely related to certain groups of algae than to other fungi, but as a matter of convenience, and in the absence of any widely accepted "natural" classification of the thallophytes, they will all be considered together. This immense array of lowly plants is much more numerous in species than the algae, and contains hundreds of types which are of the utmost importance to man and which form the subject matter of various special sciences, notably bacteriology and plant pathology.

In the general morphology both of their vegetative and of their reproductive structures the fungi parallel the algae, ranging from strictly unicellular types in the bacteria, through filamentous forms, to those which have a large and rather complex plant body; and displaying various types of sexual reproduction, both isogamous and heterogamous. In most fungi above the bacteria and slime molds, the plant body is composed of one or more filaments, each of which is known as a *hypha* (plural, *hyphae*). The whole mass of hyphae, which are often tangled or matted together, is called a *mycelium*. Special absorbing organs or

haustoria (singular, *haustorium*) are usually developed, through which the plant draws its food from the material or *substratum* on which it grows.

The series may be best divided into five classes: the Bacteria, the Slime Molds, the Alga-like Fungi, the Sac Fungi, and the Basidia Fungi.

Bacteria.—These plants differ from most other fungi in being strictly unicellular, although they may sometimes form loose colonies. The cells are usually very small, ranging from about 0.025 mm. to as low as 0.0005 mm. in length, so that bacteria are

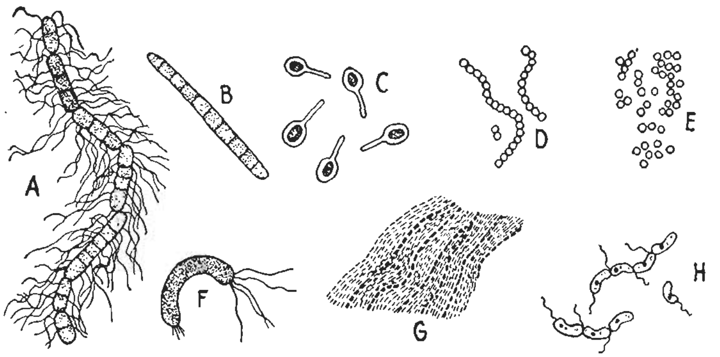


FIG. 178.—Bacteria of various types. *A*, motile individuals of *Bacillus subtilis;* *B*, non-motile individuals of *Bacillus subtilis;* *C*, tetanus cocci; *D*, erysipelas cocci; *E*, pus cocci; *F*, *Spirillum undula:* *G*, gelatinous or *zoöglaea* condition of a mass of bacteria; *H*, cholera vibrios.

the smallest of living things. Internally, these cells seem to be almost structureless. There is some evidence, however, that nuclear material and perhaps a vague nuclear body may be present, but the very minute size of bacteria makes a cytological study of them exceedingly difficult. The cell wall, which is firm, rarely contains cellulose, and seems to consist, at least in part, of *chitin.* Many species have a gelatinous outer wall. Cilia, varying in number and position, are found in many species, which thus have the power of active motility. Various structural types are recognized by bacteriologists, of which the commonest are the *coccus* form, which is spherical; the *bacterium* or *bacillus*, which is rod-shaped; and the *spirillum*, which is curved (Fig. 178). The metabolic rate of bacterial cells is very high. The only type of reproduction known is simple cell division, or fission, which is unaccompanied by any of the complex phenom-

ena found in the higher plants, but which in the presence of an abundant food supply may take place so frequently that a single cell may give rise to billions of individuals in a day's time. Bacterial cells often remain attached in chains, plates, cubes, or more complex colonies. At the onset of unfavorable conditions the protoplasm of the cell draws itself together and produces a thick-walled spore which will germinate whenever a favorable environment again ensues, sometimes after many years. Actively growing bacteria will ordinarily withstand relatively high temperatures but their resting spores are still more resistant and will often be found alive and able to germinate after hours of subjection to boiling water. They can also survive extreme cold and dryness. In their various characteristics, therefore, the bacteria (as before noted) show much resemblance to the blue-green algae.

Although bacteria occur in countless myriads of individuals and although their diverse activities make them almost omnipresent in air, water, and soil, they are so small as to be quite invisible to the unaided eye, and from a practical point of view would be entirely negligible were it not for the profound effects which they produce. Their importance in agriculture, particularly through their activity in the soil and in dairy products; their role as the chief agents of fermentation and decay; and particularly their tremendous direct interest to man as the cause of some of the worst and most prevalent of those diseases which afflict himself and his domestic animals and plants, have caused them to be studied with especial thoroughness and have established bacteriology as one of the most important of the sciences.

Exact knowledge of bacteria dates only from the latter half of the nineteenth century. Their existence was proved by the great French chemist and biologist, Louis Pasteur (Fig. 179), who labored for years, meeting with the ridicule and antagonism which often greets a new discovery, before he could convince his fellow scientists that such minute objects were actually alive and were responsible for so many of the happenings of daily life. Since Pasteur's day, as the result of a knowledge of bacteria, the practice of medicine, and to a considerable extent that of certain branches of agriculture and industry, has been radically changed; and the astonishing advances in modern surgery, made possible by Pasteur's discoveries and inaugurated by the great surgeon Lister, have converted this branch of medicine from a dreaded last

resort to a common and safe means of relief. The bacteriologist of today has developed a complicated and elaborate technique whereby he can isolate individual bacteria, cultivate them artificially on especially prepared and sterilized foods or *media* of various kinds, and study the characteristic appearance of individuals and masses, together with the physiological behavior peculiar to each. Both as the enemies and as the allies of the human race, these lowly plants with which the bacteriologist works are among the most important members of the vegetable kingdom.

FIG. 179.—Louis Pasteur, 1822–1895.

Saprophytic Types.—The saprophytic bacteria live on dead plant or animal material. They are responsible for much of the fermentation which carbohydrate substances often undergo when exposed to the air and which, as a form of incomplete respiration, has been discussed in the chapter on metabolism. *Decay*, essentially the same type of process as fermentation except that it takes place in all sorts of organic substances and is carried through to a complete break-down of these substances into carbon dioxide, water, nitrogen, and mineral salts, is brought about almost entirely through the activity of the many types of putrefactive and decay-producing bacteria. All successful methods of pre-

serving food depend on eliminating these bacteria or preventing their activity.

Pathogenic Types.—Those members of the class which are parasitic on other organisms are known as *pathogenic* bacteria. A particular species is the cause of each of the various bacterial diseases, such as diphtheria, tuberculosis, typhoid fever, pneumonia, cholera, and many others among animals and man, as well as pear blight, cucumber wilt, black rot of cabbage, and others among plants. These diseases are often communicated from one individual to another, since the pathogenic bacteria responsible for them may be transmitted easily through air, water, food, or contact. Bacteria which are very minute or otherwise difficult to recognize are also probably responsible for many diseases the cause of which is at present unknown.

The harmful effect of pathogenic bacteria on animals often is not due to the direct attack of the parasite but to the terrifically poisonous by-products, or *toxins*, which it secretes and which enter the blood. The afflicted individual will often produce *antitoxins* capable of counteracting the poisonous effect of the toxins and of rendering the individual *immune* for a time to the attack of this particular parasite. The practice of *vaccination* consists in inoculating an individual with the dead bodies of parasitic bacteria or with a virus, and thus subjecting him to a mild attack of the disease in order to stimulate the production of sufficient antitoxin in his system to confer immunity upon him for a long time. Vaccination is particularly effective against small pox and typhoid fever. The attacks of certain other disease-producing organisms may also be prevented or rendered less virulent by injecting into the circulation a little blood serum from an individual (usually a cow or horse) which has had the disease and whose blood is therefore rich in antitoxin. This *serum* or *antitoxin* treatment has been especially successful with diphtheria, tetanus, and hog cholera.

In the previous discussion of the soil two other groups of bacteria were mentioned which are of especial importance to the higher plants because of their relation to nitrogen (Fig. 20). These are the *nitrogen-fixing* bacteria, which are found in tubercles on the roots of plants belonging to the Legume family and which are able to take nitrogen directly from the air and to incorporate it into their bodies; and the *nitrifying* bacteria, which convert ammonia, the end product of protein decay, into nitrite salts and

these, in turn, into nitrate salts, the only form in which nitrogen can be utilized by most green plants.

Myxomycetes, or Slime Fungi (Fig. 180).—This remarkable group of plants is on the border-line between the plant and the animal kingdoms, but its members now are usually regarded as plants. Spores are borne in great quantities by the fruiting bodies, and each germinates into a small naked mass of pro-

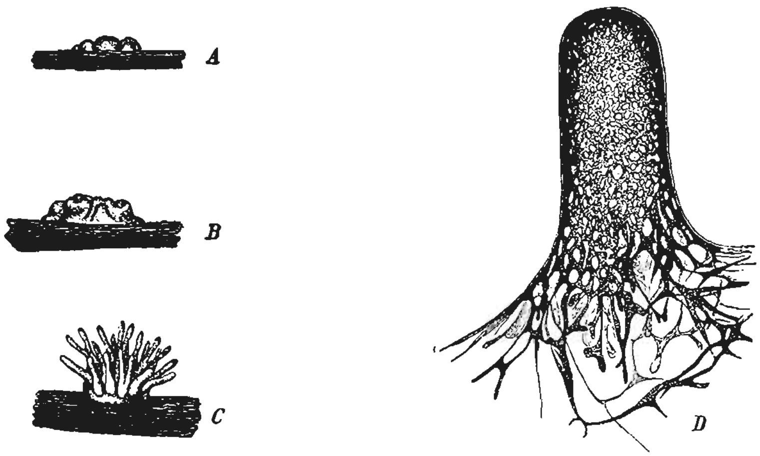


FIG. 180.—A slime mold (*Ceratiomyxa*). *A* and *B*, early stages in the development of a fruiting body; *C*, mature fruiting body, magnified about three times; *D*, plasmodium heaping itself up in the formation of a young fruiting body (*After Engler and Prantl.*)

toplasm, entirely without a wall. This is constantly changing in shape and moves slowly over the surface of solid objects by a streaming out of the cytoplasm into projecting arms or processes into which the mass of the cell finally follows. This *amoeboid* movement (so named from its resemblance to the method of locomotion of the protozoan animal *Amoeba*) is quite unlike ordinary methods of movement in plants. If water is present such a cell may abandon the amoeboid motion and develop a single cilium by which it swims actively about. It soon loses this, however, and again adopts the creeping habit. Where these naked slime-mold cells come in contact, they often fuse to form a single mass of living material, or *plasmodium*, which contains many nuclei. This absorbs food and may grow to a considerable

size, frequently many cubic centimeters in volume, and creeps about sometimes for several weeks in amoeboid fashion over damp logs and in moist and shaded places where decaying plant material is abundant. Plasmodia are often yellow or red in color. After a time, particularly if the food supply becomes reduced, the plasmodium moves out to a dryer substratum where it becomes heaped up into one or more fruiting bodies or sporangia which are perfectly definite in size and shape according to the species to which they belong. These sporangia may be rather large, rounded masses, or smaller stalked or sessile heads. The surface dries and hardens and the multinucleate mass within becomes divided into a large number of spores, each of which rounds itself off and secretes a wall. The spores are usually supported by an exquisitely delicate frame-work, the *capillitium*, and are ultimately discharged into the air.

Most slime molds are of slight economic importance, but some are parasitic. One of these, the club-root organism of cabbage, causes a serious disease of the cabbage plant.

Phycomycetes, or Alga-like Fungi.—These fungi, as their name implies, resemble rather closely certain of the algae, particularly in their methods of reproduction. They seem especially near the Siphonales because of the fact that their filaments (hyphae) are coenocytic, and it is probably from that general region of the algal series that they originated.

The Phycomycetes include a great many of the forms known as *molds* and *blights*. Three orders are particularly notable, the *Saprolegniales*, *Peronosporales*, and *Mucorales*.

Water Molds (*Saprolegniales*).—This group (Fig. 181) is entirely aquatic and in that respect, as well as in certain morphological features, shows a closer connection with its algal ancestors than do the other orders of Phycomycetes. Its members live on the bodies of dead insects and other animals and a few are parasitic, attacking fish and amphibians. A cell cut off on the tip of one of the external hyphae develops into a sporangium and liberates a large number of motile zoöspores. Sexual reproduction is heterogamous. A single-celled, spherical oögonium is developed and produces several eggs which are fertilized by the contents of an antheridium, a cell cut off on the end of a slender branch which grows out from the main hypha near the oögonium. No sperms are organized but male nuclei are carried into the eggs by delicate fertilization tubes. In

many cases the eggs develop into mature spores without having been fertilized at all.

Blights and Downy Mildews (*Peronosporales*).—The species composing this group (Fig. 182) are all parasites on the higher plants. Their spores germinate on the surface of the leaf or

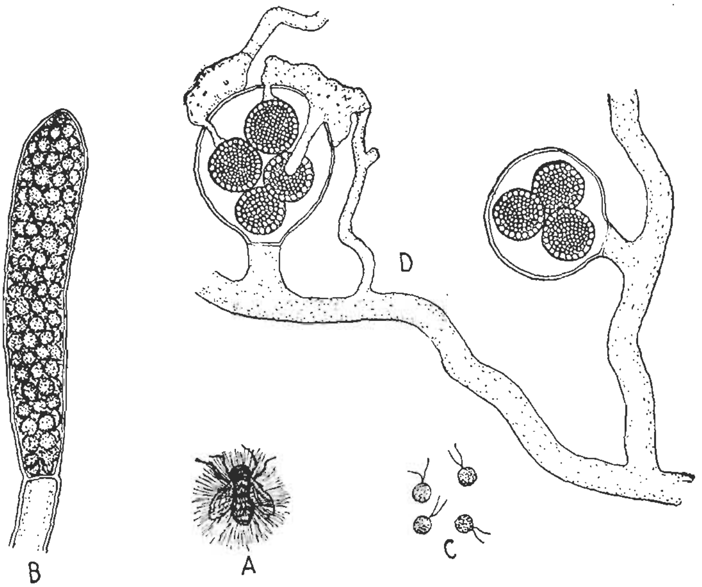


FIG. 181.—*Saprolegnia*, one of the Saprolegniales. *A*, mycelium on an insect in water. *B*, terminal sporangium producing zoöspores. *C*, zoöspores. *D*, sexual organs; the two oögonia each containing several eggs. The one at the left has been penetrated by antheridial filaments.

stem and, entering the tissues, branch through them in all directions, absorbing food and often causing the death of the host plant. Definite fruiting bodies are produced at the surface of the various organs of the host, where specialized hyphae become constricted to form spores, which separate and are carried away by the wind. Non-sexual aerial spores produced in this manner are called *conidia*, and are of frequent occurrence among fungi. Sexual organs appear in the deeper tissues. The egg nucleus in the oögonium is fertilized by a male nucleus from an adjacent antheridial filament, and a thick-walled oöspore is formed. At germination, the contents of this oöspore divides inside the oöspore wall to form many biciliate zoöspores, doubtless retaining this method of germination from an algal ancestor, though the plant has otherwise become specialized as a leaf

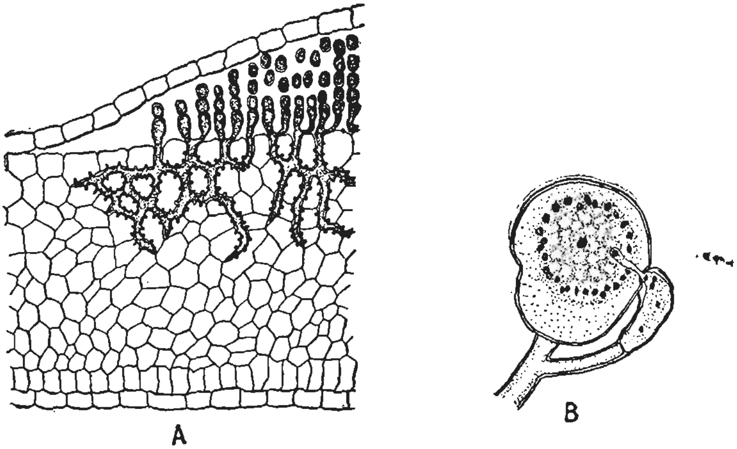


FIG. 182.—*Albugo*, one of the Peronosporales. *A*, section through a leaf-blade showing portion of a "blister" produced by the fungus. The hyphae penetrate between the cells of the leaf, sending into them small, sucker-like structures. Under the *epidermis* are produced rows of conidia. *B*, sexual organs, the antheridial filament (at right) discharging a male nucleus into the oögonium, at left.

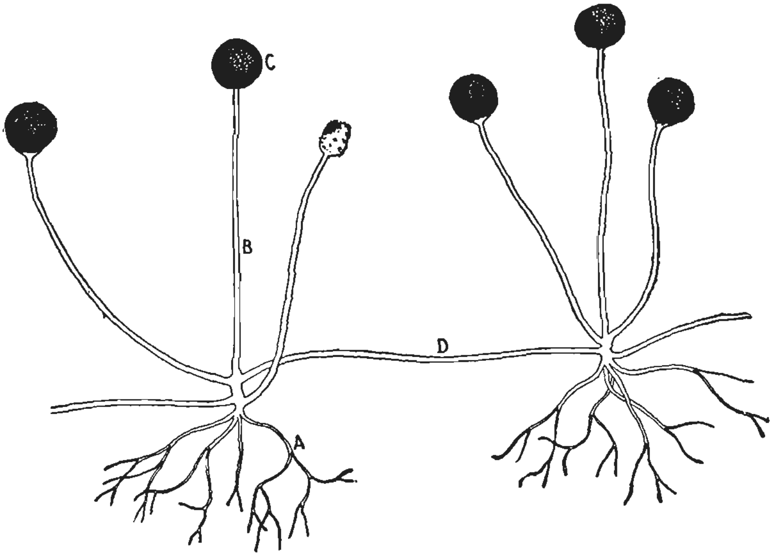


FIG. 183.—The bread mold (*Rhizopus*). General habit of the plant. The mycelium (*A*) of much-branched hyphae penetrates the substratum and sends up into the air stouter hyphae, the *sporangiophores* (*B*), on which are borne the spherical sporangia (*C*). One sporangium has burst, shedding its spores, a few of which still adhere to the central axis or *columella* of the sporangium. The two groups of sporangiophores are connected by a *stolon* (*D*).

parasite. Such destructive plant parasites as the potato blight and the grape-vine mildew belong to this order.

True Molds or Black Molds (*Mucorales*).—These fungi (Fig. 183) are very common on moist, decaying organic material such as manure, rotting fruit, and the like. Their white, cobwebby mycelium, composed of much-branched hyphae, freely penetrates the substratum in all directions. From the surface, stout hyphae arise into the air and bear at their tips globular sporangia

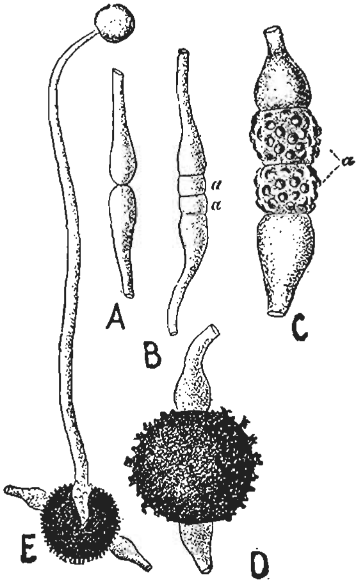


FIG. 184.—Sexual reproduction in *Mucor*. *A*, two conjugating hyphae in contact; *B*, a gamete, (*a*) cut off from the end of each hypha; *C*, the enlarged gametes; *D*, thick-walled zygospore which has arisen from the union of the two gametes; *E*, zygospore germinating to produce a sporangium. (*From Strasburger, after Brefeld.*)

which burst and liberate masses of dark-colored, non-motile spores, each of which may germinate directly into a new plant. These spores are probably homologous with zoöspores, but motility has been lost in this group because of the assumption of the aerial habit of growth. Sexual reproduction is isogamous or essentially so (Fig. 184). Two short branches or *suspensors*, arising from adjacent hyphae, approach one another and come into contact end-to-end. From the tip of each is cut off a single multinucleate cell which is the gamete, and these two adjacent

gametes fuse to produce a thick-walled zygospore. It has been found that two distinct sexual strains often exist, entirely similar outwardly but functioning quite differently in reproduction. These have been called the *plus* and *minus* strains and correspond to the two sexes, for zygospores are usually produced only when a *plus* plant and a *minus* plant come into contact. These fungi furnish an interesting example of a physiological differentiation of sex which is not accompanied by morphological differences.

Ascomycetes, or Sac Fungi.—This enormous group of plants includes over 20,000 species. They show but little resemblance to the algae, and although all must have come originally from some chlorophyll-bearing forms, their exact ancestry is not clear. These fungi are typically land-inhabiting plants and include both saprophytic and parasitic species. Both groups differ from the Phycomycetes in the fact that their hyphae are divided into cells by cross-walls, and that sexual processes are much reduced or altogether lacking. The plant body commonly consists of a much-branched mycelium extending throughout the substratum, and a definite *fruiting body* which is developed at the surface. Each group displays a rather specialized method of spore formation.

The ascomycetes are distinguished by their production of spore sacs or *asci* (singular, *ascus*) in each of which are borne (ordinarily) eight spores, the *ascospores,* surrounded by some cytoplasm not used up in their formation (Fig. 185). A group of asci are generally imbedded in a mass of sterile hyphae and partially or completely surrounded by a protective envelope of compact mycelium. Such a fruiting body is known as an *ascocarp.* In many cases, this ascocarp has been found to originate as the result of a sexual union deep in the mycelium, the whole process bearing a considerable resemblance to that found among the red algae. In some other cases the sexual organs appear to be reduced or altogether suppressed. The ascomycetes include an immense variety of types, only a few of which can be mentioned here.

Cup Fungi (Pezizales).—Throughout this order (Figs. 186 and 187) the ascocarp is a broad disc, cup, or funnel, and the name Discomycetes or disc fungi is therefore often applied to the group. The inner surface of the cup consists of a layer of asci and sterile hyphae. Such a layer is known as the *hymenium.* These

plants are almost all saprophytes and their brightly colored fruiting bodies are conspicuous on rotting logs, damp earth, and similar situations.

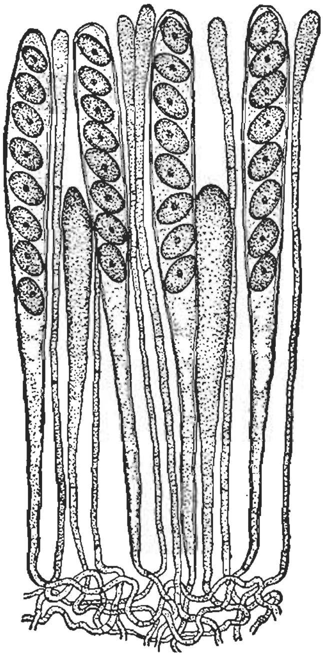


FIG. 185.—Spore production in an ascomycete. Portion of the hymenium, or fruiting surface, of *Peziza*, showing the asci, each with eight ascospores. Among the asci are slender, sterile hairs, or paraphyses, and two young asci.

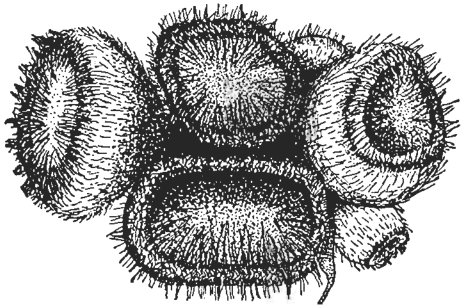


FIG. 186.—*Peziza ciliata*. The cup-like ascocarps, on the inner surface of which the asci are borne.

Related to the cup fungi are the Morels (*Helvellales*), which develop large, fleshy, and edible fructifications, the fruiting surface of which is broken up into irregular pockets; and the

Truffles (*Tuberales*), which produce subterranean, tuber-like ascocarps, usually associated with the roots of oak trees, and much prized as delicacies.

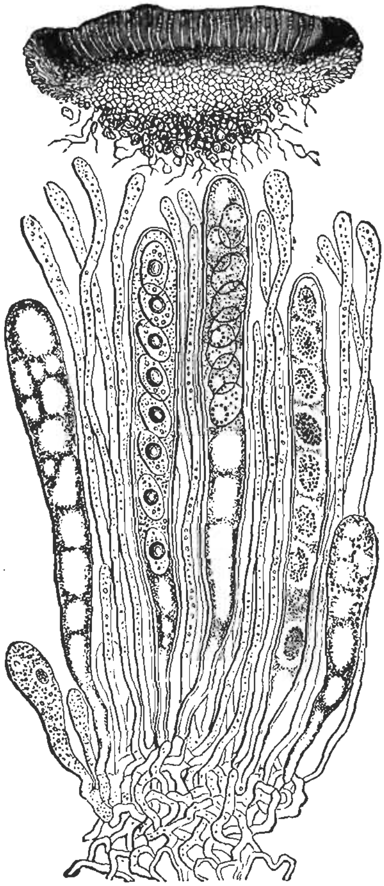


FIG. 187.—*Humaria convexula.* Above, cross section through the fruiting body. Below, a portion of the hymenium much enlarged showing asci and paraphyses. (*After Sachs.*)

Black Fungi (*Pyrenomycetes*).—Here are found a large and varied group of fungi which include both parasitic and saprophytic species. Their mycelium is often hard and compact and is characteristically dark in color. The ascocarp consists of a very small, flask-shaped structure, the *perithecium* (Fig. 188), lined with a hymenium and opening to the air by a minute pore.

Here belong the knot and wart fungi found on so many woody plants, some of which, such as the "black knot" of plums (Fig. 189), are serious parasites. In this order also occur the destructive chesnut bark fungus and other important disease-producing organisms.

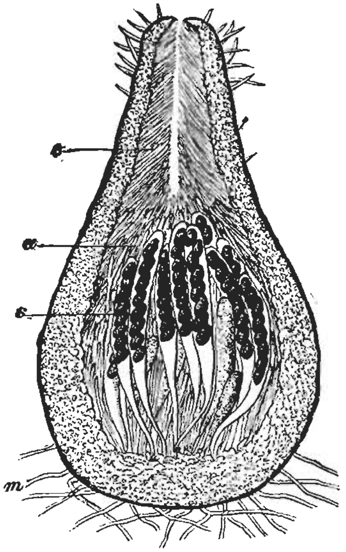


FIG. 188.—*Podospora fimiseda*. Longitudinal section through a perithecium, showing asci. (*After Tavel.*)

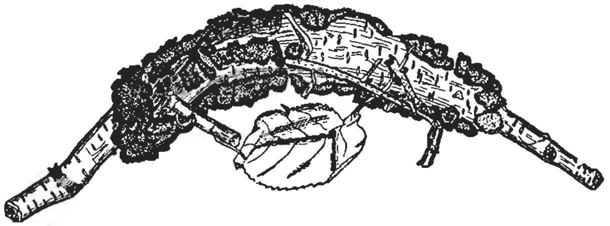


FIG. 189.—*Plowrightia morbosa*, the "black knot" of plums and cherries. Hard, black fruiting mass of the fungus on a twig which it has attacked. The small dots are openings to the perithecia.

Mildews (*Erysiphales*).—These small fungi develop a cobweb-like mycelium which spreads over the surface of the leaves of many plants and is parasitic on their epidermal cells. Conidia are produced in abundance.

In these forms the asci have been shown clearly to develop as the result of a sexual union (Fig. 190). From two adjacent

hyphae arise specialized branches which lie next each other in pairs. The tip of each of these, containing a single nucleus, is cut off by a cross-wall. One of these cells is markedly smaller than the other, and is the equivalent of an antheridium bearing a single male gamete. The larger cell is an oögonium or carpogonium, bearing a single egg. The wall between these two sex organs breaks down and the male gamete enters the oögonium, where the nuclei of the two gametes unite. The fertilized egg divides into a group of cells and on branches arising from these cells the asci develop.

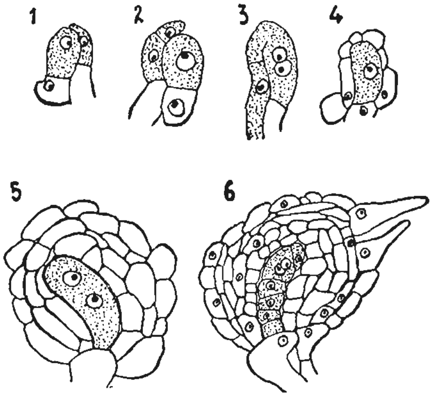


Fig. 190.—Sexual reproduction in an ascomycete (*Sphaerotheca*). 1 and 2, antheridium and oögonium in contact; 3 and 4, fertilization; 5 and 6, development of the young perithecium, the fertilized egg producing a group of cells from which asci ultimately arise. (*After Harper.*)

Blue and Green Molds (*Plectascales*).—Here are found the common molds (aside from the Mucorales) which appear on bread, cheese, leather, and almost all organic substances which will "mold" when subjected to dampness (Fig. 191). Their abundant masses of conidia are typically greenish or bluish in color. Small, spherical ascocarps, full of irregularly scattered asci and lacking a hymenium, are occasionally produced. No members of the order are parasitic, but a few are of economic importance in cheese manufacture and in other ways.

Yeasts (*Saccharomycetes*).—These minute plants (Fig. 192) are usually regarded as reduced ascomycetes. The individual is a single cell, possessing a definite nucleus, cytoplasm, and sap-cavity and producing, by the process of "budding," a loose, irregular chain of cells. When conditions become unfavorable,

the contents of some of the cells divides into four spores, forming a structure which is believed to represent a modified ascus. The yeasts are saprophytes on sugary substances, thriving in the

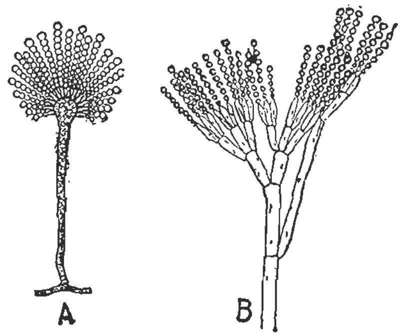


FIG. 191.—*Aspergillus* (*A*) and *Penicillium* (*B*). Hyphae bearing chains of air spores or conidia. (*From Strasburger.*)

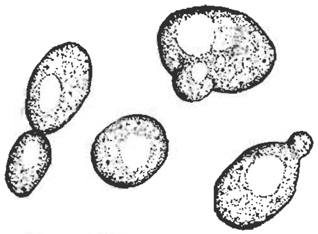


FIG. 192.—Yeast (*Saccharomyces*). Single-celled plants in various stages of division or budding.

absence of free oxygen, and are the chief agents in alcoholic fermentation, a process which has been described in a preceding chapter. Their use in the raising of bread is familiar.

Basidiomycetes, or Basidia Fungi.—Like the ascomycetes, this is a very large and varied group. Its specialized reproduc-

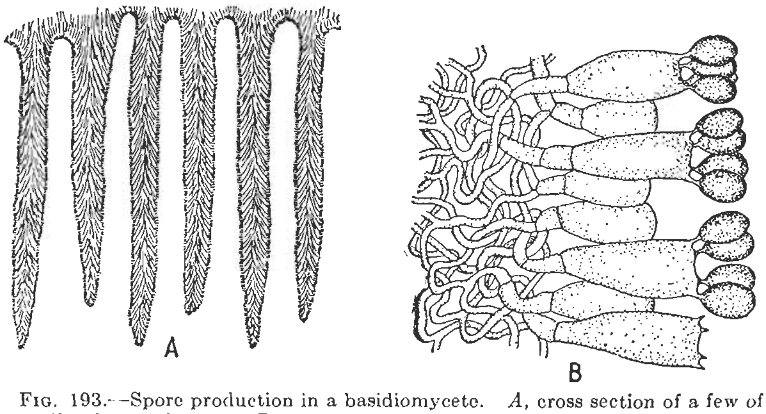


FIG. 193.—Spore production in a basidiomycete. *A*, cross section of a few of the gills of a mushroom. *B*, a portion of the surface of one of the gills, much enlarged. The stout cells are basidia. Each of these bears four basidiospores on slender stalks or sterigmata. The lowest basidium has shed its spores.

tive structure, the *basidium* (Fig. 193), is the swollen terminal cell of a hypha and typically bears four *basidiospores*, each supported on a delicate stalk or *sterigma* (plural, *sterigmata*). The basidia

are arranged in a more or less definite fruiting surface or hymenium. Aside from this difference in the method of spore production, the group as a whole is distinguished from the ascomycetes by the apparent rarity of sexual processes and by its larger and more conspicuous fruiting bodies. The basidiomycetes are regarded as the highest of the fungi and are believed to have come from ascomycetes, the basidium representing a much modified ascus.

A few orders, notably the Smuts (*Ustilaginales*) and the Rusts (*Uredinales*) differ from the typical basidiomycetes (or *Autobasidiomycetes*) in having basidia (or structures thought to represent basidia) which instead of being one-celled are composed of three or four cells, each producing a spore.

Smuts (*Ustilaginales*).—Here are found a number of destructive parasites which attack floral organs, especially among members of the Grass family. The mycelium spreads through the body of the host plant and at flowering time gathers in dense masses, particularly in the ovaries and surrounding tissues, which are swollen and distorted and form the so-called "smut." The mycelium here becomes transformed directly into a mass of black, thick-walled spores which survive the winter. On germinating the next spring, each spore produces a short filament of three or four cells, the *promycelium*. This promycelium is thought to represent a basidium, for each cell bears one or more spores or *sporidia,* which are capable of infecting new plants. The smuts of corn, oats, and wheat are particularly destructive.

Rusts (*Uredinales*).—All members of this order are parasites, often becoming very destructive, and have the most complicated life histories of any of the fungi.

The common wheat rust, *Puccinia graminis* (Fig. 194), is the best known member of the group. The mycelium of this species, in the tissues of the wheat plant, consists of binucleate cells. It breaks through the surface and produces clusters of one-celled, reddish, rough-walled spores, the summer spores or *uredospores,* which give a rust-like appearance to the stems and leaves. Each uredospore may be borne by the wind or other means to another wheat plant where it germinates and produces directly a new mycelium. Toward the end of the season, clusters of another type of spore are produced at the surface of the plant. These are black, two-celled, and heavy-walled, and are known as winter spores or *teleutospores.* They live over the winter and in the

following spring each cell germinates into a slender, four-celled, saprophytic promycelium somewhat as in the smuts. Each of

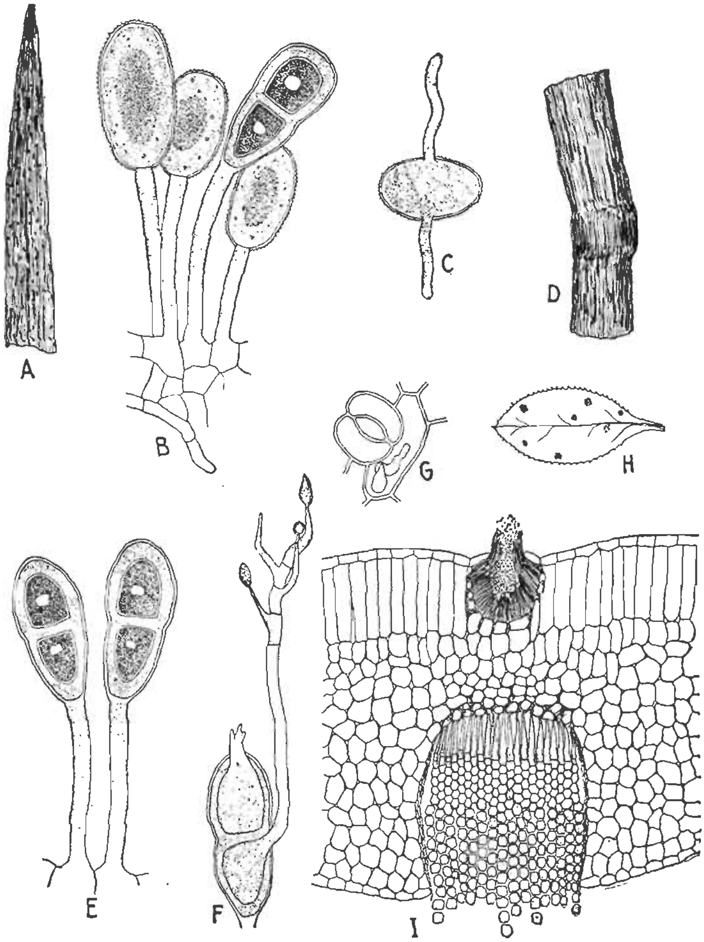


FIG. 194.—*Puccinia graminis*, the wheat rust. *A*, wheat leaf with groups of summer spores (uredospores). *B*, uredospores (one teleutospore among them). *C*, germinating uredospore. *D*, wheat stem with masses of winter spores (teleutospores). *E*, two teleutospores. *F*, germinating teleutospore, producing a promycelium on which are borne the sporidia. *G*, sporidium germinating on epidermis of barberry leaf. *H*, lower surface of barberry leaf, showing cluster-cups or aecidia. *I*, section through the leaf of barberry showing spermagonium on upper surface and aecidium on lower. The aecidium is producing masses of aecidiospores, which infect wheat plants. (*B*, *C*, *F* and *G* after *De Bary*.)

the cells here produces but a single sporidium, however, so that the structure displays a closer resemblance to a typical basidi-

um. The remarkable fact has been demonstrated that these sporidia (or basidiospores) do not infect wheat, but will attack only plants of the barberry. The spores germinate on the barberry leaves, and the hyphae penetrate the tissues, producing there a vigorous mycelium which is now composed only of uninucleate cells. On the upper surface of the leaf soon appear small flask-shaped structures, the *spermagonia,* in which are formed enormous numbers of very minute cells or *spermatia.* As its name implies, this organ has been thought to represent the male sexual apparatus; and the spermatia closely resemble those of the red algae, from which group the rusts are believed to have arisen. Whatever its original share in the life cycle may have been, however, its present function is obscure, though recent investigations indicate that it may have some significance in the life history. On the lower surface of the barberry leaves are formed cluster-cups or *aecidia* (singular, *aecidium*), flaring, cup-shaped structures, from the base of which, and as the result of sexual unions between adjacent cells, arise long rows of *aecidiospores.* These, in turn, never reinfect barberry but attack only wheat plants, thus completing the life cycle.

Many other rusts resemble this species in alternating between two distinct hosts, and are termed *heteroecious;* but some are confined entirely to one host. The rusts produce many serious plant diseases, among them the white-pine blister rust, which has its uredo-stage on currants and gooseberries; the apple rust, which has its teleuto-stage on red cedar; and many others.

The typical or true basidiomycetes, or *Autobasidiomycetes,* include two main sub-classes: the *Hymenomycetes,* in which the fruiting surface or hymenium is exposed to the air; and the *Gasteromycetes,* in which it is enclosed within the tissue of the fructification. These are both chiefly saprophytic, the extensive mycelium penetrating the substratum deeply and under favorable conditions producing at the surface very characteristic fructifications or *sporophores.* Enormous numbers of spores are produced, the output of a single giant puff-ball having been estimated at 7,000,000,000,000 spores.

Hymenomycetes.—These fungi are divided into a number of orders, but by far the most important are the *Agaricales* or agarics, which include the mushrooms and toadstools. This is a very large group and includes the most important of the so-called 'fleshy fungi." Because of the edibility of the sporophore of

many of its members and the poisonous character of a few of them, the Agaricales have received intensive study and are more widely known than any other fungi.

The order is divided into a number of families according to the type of fruiting body produced. In the Agaricaceae or gill fungi (Figs. 195, 196, and 197), which are the mushrooms and toadstools proper, the hymenium covers the surface of plate-like

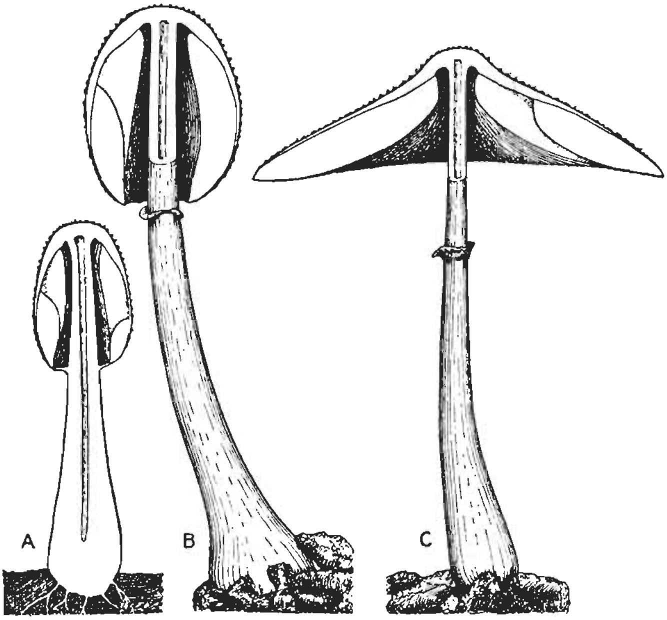


Fig. 195.—The fruiting body of a basidiomycete (*Lepiota*.) Longitudinal sections of three stages, showing the stalk or stipe, the broad cap or pileus, and the gills which hang from the under surface of the latter. At *A* the young fructification is still surrounded by a membrane, the *volva*, which breaks as the pileus expands and the remains of which can be seen as a ring around the stipe. (*From Buller. "Researches on Fungi."*)

structures or *gills*. The sporophore in this group is the typical "toadstool," which consists of a stalk or *stipe* supporting a broad cap or *pileus*, from the under surface of which hang the gills. A few of the species are regularly cultivated and constitute a food product of some importance. A number are poisonous, and the amateur mushroom collector is always in danger of adding them to his menu. In the *polypores* (Polyporaceae, Fig. 198) the hymenium lines narrow tubes which open by pores on the surface

of the pileus. These include many mushroom types as well as the hard, bracket-like forms so common on rotting logs, which are very destructive of wood and are sometimes parasites upon living trees. In the Tooth fungi (Hydnaceae) the hymenium covers the surface of tooth-like or spine-like projections.

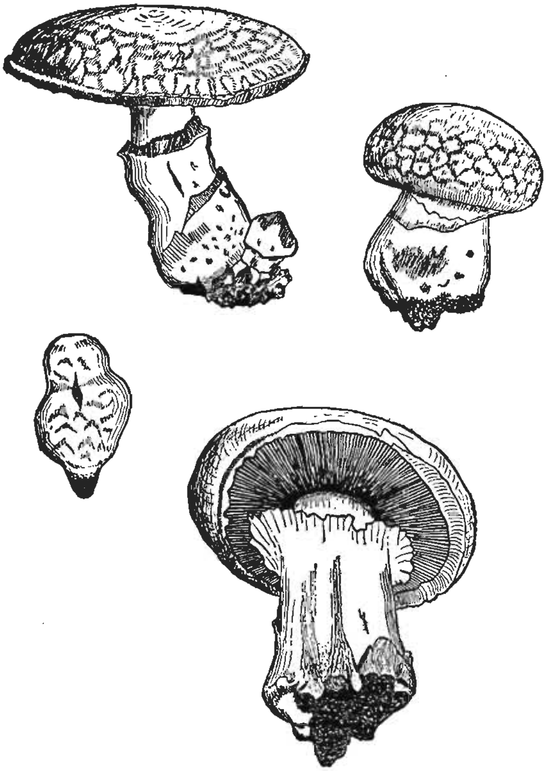


FIG. 196.—The common mushroom, *Agaricus campestris*. Views of developing and of mature fructifications.

Close to the Agaricales are the Coral fungi (*Clavariales*), the much-branched sporophores of which are covered by the hymenium.

Gasteromycetes.—These are the highest of the fungi. Their fructification in general is a rounded mass of hyphae, the outermost layer of which becomes differentiated into a cortex or *peridium*, surrounding the inner mass of hyphae and basidia which is called the *gleba*. Two important orders are the *Lycoperdales* and the *Phallales*.

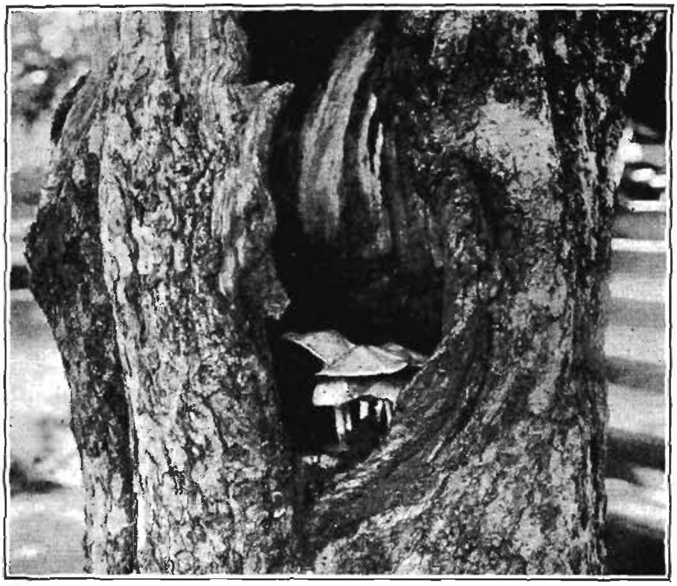


FIG. 197.—A gill fungus growing in a hollow tree. The mycelium penetrates the wood in all directions and has produced the fruiting bodies here shown. In cases like this it is sometimes hard to tell whether the fungus is a parasite or a saprophyte.

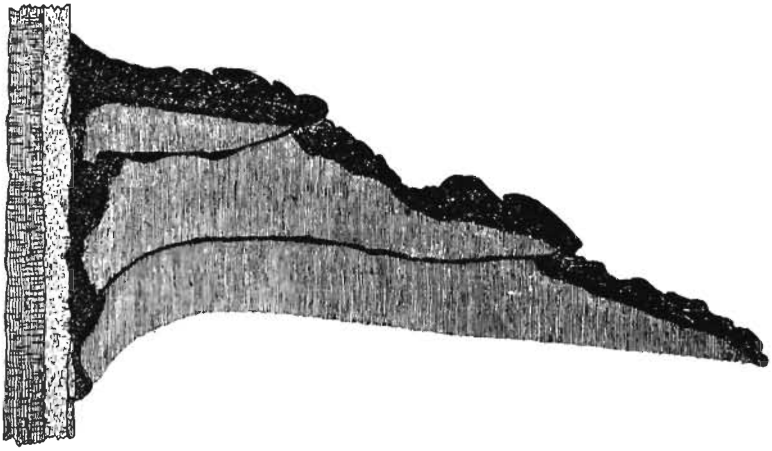


FIG. 198.—Section through the bracket-like fruiting body of a polypore (*Fomes applanatus*) showing three annual layers. The spores are produced on the lining of the minute tubes and drop out through the pores into the air. (*From Buller, "Researches on Fungi."*)

Puffballs (*Lycoperdales*).—The sporophore in these fungi (Figs. 199 and 200) is a globular structure which in some species becomes very large and which is usually edible when young. At maturity

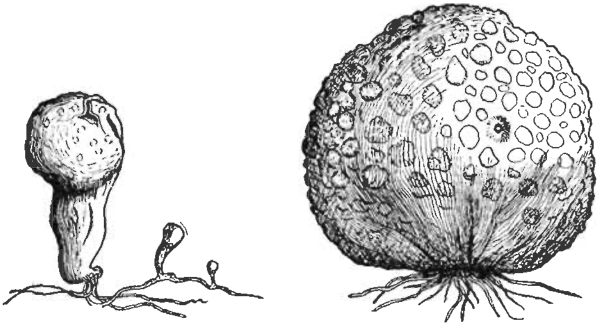


FIG. 199.—Puff-balls. General appearance of young and of mature fructifications.

FIG. 200.—Saprophytic fungi. Coral fungi, above, and young puff-balls, below. In the photograph are also ferns, lycopods, and leafy liverworts.

the peridium breaks open at the top and a mass of dark spores is discharged through it.

Stink-horns (*Phallales*).—The gleba here ripens into a foul-smelling mass, breaks through the peridium, and is pushed

upward at the end of a stalk (Fig. 201). The rank odor attracts to these fungi many carrion-loving insects.

Lichens.—In addition to the algae and fungi proper, the thallophytes include a remarkable group of composite plants, the *lichens.* These are fungi in the mycelium of which groups of algal cells are entangled (Fig. 202). The advantage to the fungus of this intimate association is evident, and the alga is also probably benefited to some extent. Instead of regarding this as a case of true symbiosis, however, most botanists look upon the fungus as parasitic on the algal member of the combination, even though this parasitism is very mild. The two component plants have been artificially separated, and it has been found that the alga can exist independently in every case but that the fungus is unable to do so. Lichens also have been "synthesized" experimentally by bringing appropriate algae and fungi together. The fungus members of lichens are almost always ascomycetes. A number of different algae are represented in lichens but these belong mainly to the Cyanophyceae and to the Chlorophyceae. All are very simple in character. The fungus mycelium is often somewhat gelatinous and thus tends to absorb water readily and hold it tenaciously. It is much more compact, differentiated, and definite in shape than that of ordinary fungi and is essentially a flat thallus (Fig. 203). Three main types of thallus are recognized: the *crustaceous*, which grows closely appressed to the surface of rocks, bark, and similar structures; the *foliose*, in which the thallus is broader and somewhat branched, suggesting that of the liverworts; and the *fruticose*, in which it is slender and very much branched and may be either erect or hanging.

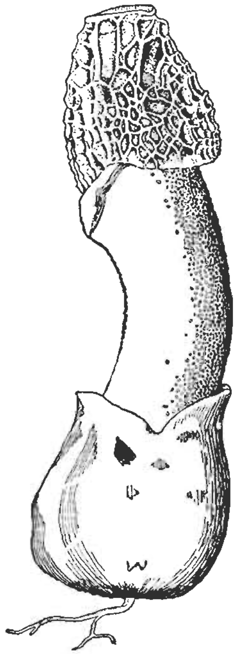


FIG. 201.—*Phallus*, the stink-horn. Fruiting body, showing the gleba above, at the end of the stalk, and the remains of the peridium below.

Asexual multiplication is accomplished by the production and dispersal of *soredia* or small bits of mycelium in which a few algal cells are entangled. The fructifications are conspicuous, and the

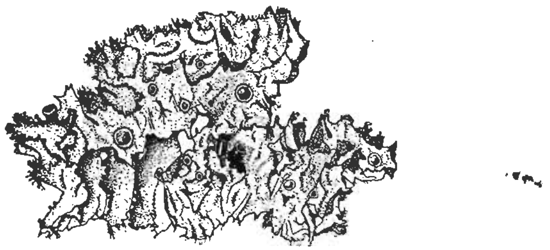


FIG. 202.—A lichen (*Parmelia*), showing the rather thin and thallus-like character of the plant body and the cup-shaped sac-fruits or ascocarps.

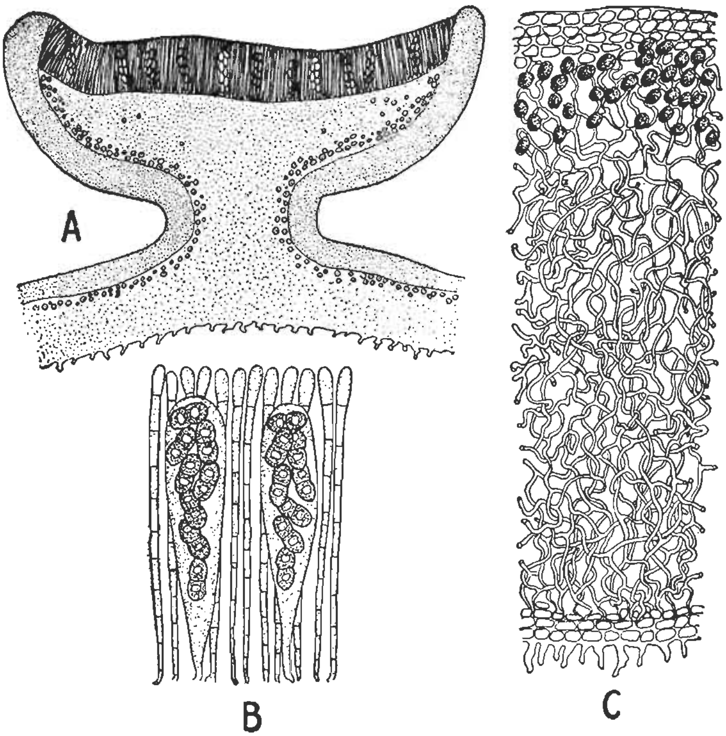


FIG. 203.—*Physcia stellaris*, a lichen. *A*, section through an ascocarp, showing fruiting-surface (hymenium) of asci and sterile hairs; *B*, a portion of the hymenium enlarged, showing two asci and several paraphyses; *C*, section through the thallus, showing the mass of mycelial filaments and (near upper surface) a group of algal cells imbedded in the mycelium.

ascocarps are usually either cup-shaped or disc-shaped, as in the Discomycetes (Fig. 202, *A*). Definite and functional sex organs, strongly suggestive of those in the red algae, have been demonstrated in certain species.

Lichens usually are xerophytic and will thrive on bare rocks and exposed places where no other vegetation can exist. Their importance in nature is therefore considerable, but they include only a few species which are of direct economic value to man.

QUESTIONS FOR THOUGHT AND DISCUSSION

593. The thallophytes are the most varied in their characteristics of all the main divisions of the plant kingdom. What reason can you suggest for this fact?

594. In what way (or ways) is the classification of the thallophytes presented in this text an artificial one?

595. All groups of algae are found in the ocean but comparatively few in fresh water. Explain.

596. Zoöspores of algae will generally swim toward the light rather than away from it. Of what advantage is this to the plant?

597. Unicellular algae are frequently spherical in form, but among larger types the body is never a solid sphere. Explain.

598. Algae are in general much more filamentous and finely branched than land plants. Explain.

599. Algae which are completely and somewhat deeply submersed all the time are much more finely branched and dissected than those which are near the surface or are partially exposed to the air for some of the time. Explain.

600. Are algae commoner on a rocky coast or a sandy one? Explain.

601. Sea-weeds which grow between tide-marks are often very gelatinous. Explain.

602. The largest of the algae are usually found in cool northern seas rather than in warm tropical ones. Explain.

603. There are no living algae or other green plants at depths greater than a few hundred feet below the surface of the ocean. Explain.

604. Since no green plants can live in the deeper portions of the ocean, how is it possible for fish and other animals to exist there?

605. Why are very shallow parts of the ocean, like the Grand Banks of Newfoundland and the North Sea, such important fishing grounds?

606. The algal flora near shore, and especially near the mouths of large rivers, is very rich. Explain.

607. What advantages and what disadvantages have those algae which float freely in the water (the plankton) as compared with those which are attached to a substratum?

608. What important element in the food supply of man has its source in the algae?

609. Blue-green algae can thrive in relatively dry places as compared with other algae. What structural peculiarity of theirs makes this possible?

610. Blue-green algae are generally found in waters which are rich in organic matter. What does this suggest as to differences between their methods of nutrition and those of ordinary green plants?

611. Blue-green algae can thrive in hot springs and in warmer waters generally than can most of the other algae. What explanation can you suggest for this fact?

612. What is there in the present distribution of *Spirogyra* and its allies which suggests that they are less ancient than most other green algae?

613. In *Spirogyra,* which of the gametes would you regard as male and which as female? Explain.

614. Why does *Pleurococcus* grow most abundantly on the north rather than on the south side of tree trunks?

615. What is meant by the expression that one group of plants is "on the direct line of ascent" to another?

616. Why is it generally believed that the green algae rather than the other algal groups are on the direct line of ascent to the bryophytes?

617. What are the advantages and the disadvantages of the coenocytic condition?

618. It has been suggested that there may be a typical alternation of generations in *Ectocarpus*, as there is in *Laminaria*. On the basis of the facts given in the text, outline a life history for *Ectocarpus* which would show such an alternation.

619. What are the advantages conferred by the possession of bladder-like floats in the brown algae?

620. How does the method of growth of the thallus of *Fucus* differ from that of most algae and somewhat resemble that of stem growth in the higher plants?

621. In what respect is fertilization in *Fucus* different from that in any other alga described in the text?

622. What group of green algae do you think the Diatoms most resemble? Enumerate the points of resemblance.

623. Why is it generally believed that fungi have evolved from algae rather than algae from fungi?

624. There are many more species of fungi than of algae. Explain.

625. Why is it that most fungi inhabit the land and most algae the water?

626. Is wind or water the commoner agency for the distribution of the spores of the algae? of the fungi?

627. Why are the numbers 2, 4, 8, 16, 32, and 64 so common in the production of spores, gametes, and similar bodies?

628. What is the advantage of the thick wall commonly found in zygospores and oöspores?

629. Why are so many fungi edible, but so few algae?

630. Why are fungi so much more important economically than algae?

631. What steps can you suggest through which the parasitic habit in fungi may have arisen?

632. Spores of a given species of parasitic fungus will generally germinate and grow only on one or at most a few host plants. What is there analogous to this selective action in any of the other physiological activities of plants?

633. Why are the fungus diseases of plants so much more common in the United States now than they were two hundred years ago?

634. Why is a wound much more liable to attack by fungi than is a healthy area?

635. Why are fungus diseases usually more prevalent in wet weather than in dry?

636. Why is a spray of such substance as copper sulphate effective in preventing fungus attacks on plants?

637. How do you explain the fact that a piece of moist bread shut up in a box will almost always develop mold?

638. Why should it be that the bacteria are the commonest disease-producing parasites in animals, but that the higher fungi are the most important causes of disease among plants?

639. What various means can you suggest for combatting the fungus diseases of crop plants?

640. What characteristic difference between insects and fungi, as to the environmental conditions under which they thrive best, makes it rather unlikely that fungus parasites of insects can ever be very widely employed to combat insect pests?

641. What evidence is there that bacteria are plants rather than animals?

642. What evidence can you find from the facts presented in the text that bacteria have descended from blue-green algae? that they have descended from the flagellates?

643. The very minute size of bacteria is thought to be one reason why they are able to maintain such a very high degree of physiological activity. Explain.

644. If a bacterium divides every half hour, and its descendants divide at the same rate, approximately how many descendants would it have at the end of twenty-four hours? (You can answer this readily by the use of a table of logarithms.)

645. What is the reason that such prodigious rates of increase as indicated by the previous question actually occur but rarely?

646. Why cannot plants be readily treated with serums and vaccines, as animals can?

647. Algae themselves are not harmful in drinking water but their abundance therein is often a sign that such water may be dangerous to drink. Explain.

648. Why is it important to boil surgical instruments before using them in an operation?

649. Why are coughing and sneezing particularly dangerous as means of spreading infection?

650. Pasteur found that a sample of air taken in Paris contained many bacteria but that one taken in the high Alps was free from these organisms. Explain.

651. Why will food keep longer in cold storage than under ordinary conditions?

652. Why do not dried vegetables and meats decay?

653. Name at least five different methods which are employed to preserve food and keep it from decaying, and state what makes each method effective.

654. In what respects do slime molds resemble animals? In what respects do they resemble plants?

655. Of what particular interest are slime molds in a study of the problems of the organization and differentiation of the plant body?

656. What group of algae does *Rhizopus* most resemble in its reproduction?

657. What forms among the algae do the Mucorales resemble in possessing plants which look alike but are entirely different sexually?

658. Some kinds of fungi, notably the truffles, grow only near certain species of forest trees. What explanation for this fact can you suggest?

659. Why are teleutospores thicker-walled than uredospores?

660. What simple means can you suggest for the eradication of wheat rust from a given region?

661. What conditions favor the luxuriant growth of mushrooms and toadstools?

662. Of what advantage to the fungus is the production of the "toadstool" type of fruiting body?

663. What are the advantages of the gills, pores, and teeth commonly present in the fruiting bodies of the fleshy fungi?

664. Of what use to the stink-horn fungus is its carrion-like odor?

665. In general, what insects are the commonest carriers of fungus spores? Explain.

666. In a lichen plant, what is the advantage gained by the fungus and what by the alga?

667. How different, in general, is the substratum on which lichens grow from that which supports algae or fungi? Explain.

668. Lichens are greener when moist than when dry. Explain.

669. The vegetative body of a lichen is more thin and thallus-like than that of most of the fungi. Explain.

670. Why should it be that the algal members of most lichens are either blue-green or green algae, and never are brown or red algae?

671. What conditions must be present before an ascospore produced by a lichen plant can give rise to a new lichen plant?

672. Of what importance are lichens in the economy of nature?

673. Aside from lichens, what other instances do you know in the plant kingdom where fungi become intimately associated with green plants?

REFERENCE PROBLEMS

168. Name as many algae as you can which are of direct economic importance.

169. Describe the characteristics of the Flagellates.

170. What evidence is there that the brown algae are more closely related to the Flagellates than to the green algae?

171. What is "diatomaceous earth," and how was it produced?

172. In what important sense are the tissues of a fungus *fructification* unlike the tissues of a seed plant?

173. Give the life history of some important fungus disease not mentioned in the text.

174. Enumerate and describe all the various methods of spore formation found in the fungi.

175. Give an example of a change in some agricultural practice which has come about since the existence and importance of bacteria have been recognized.

176. Species of bacteria which look alike may often be distinguished from one another by differences in their physiological activity. How are these differences shown? What examples can you cite from seed plants of the use of physiological differences to distinguish plants which look much alike?

177. What is a "filterable virus"? Give an example of one.

178. What bacteria are there which do not live on the organic material produced by green plants but derive their energy from other sources?

179. Describe the life history of the organism causing club-root of cabbage.

180. Give some examples of the "physiological races" which have been discovered in certain species of the rust fungi, and explain the economic importance of such races.

181. Describe in detail the life history of some heteroecious rust not mentioned in the text.

182. What are fungus galls, and how are they produced? Give some examples of them.

183. Describe the methods by which edible mushrooms are ordinarily grown for the market.

184. What general rules may be observed for distinguishing poisonous fungi from edible ones?

185. What are "fairy rings" and how may they be explained?

186. What are truffles? Where do they grow? How are they gathered?

187. What plant is believed to have been the "manna" eaten by the Israelites in the wilderness? (Exodus 16:14–35; Numbers 11:6–9.)

188. Who first discovered that lichens are composed of algae and fungi? Who first made a "synthetic" lichen?

189. Name as many lichens as you can which are of direct economic importance.

190. Give the author and title of three important books on the algae, and outline briefly the content of each.

191. Give the author and title of three important books on the fungi, and outline briefly the content of each.

192. Name several botanical investigators who have done important work on the algae, and state the notable contributions made by each.

193. Name several botanical investigators who have done important work on the fungi, and state the notable contributions made by each.

194. Give the derivations of the following terms and explain in what way each is appropriate:

Heterocyst	Pyrenoid	Basidium
Zoöspore	Plankton	Perithecium
Zygospore	Trichogyne	Hymenium
Oöspore	Mycelium	Sterigma
Heterogamy	Conidium	Teleutospore
Antheridium	Ascus	Uredospore
Oögonium	Soredium	Aecidium

CHAPTER XIV

THE BRYOPHYTA

The second of the four great divisions of the plant kingdom consists of the *Bryophyta*, or bryophytes, the members of which are known commonly as the liverworts and mosses. This group is much smaller than the thallophytes, containing only about 16,000 species, nor does it approach them in the diversity of plant types which it displays. All of its members are lowly and inconspicuous, the tallest mosses rarely attaining a decimeter in height. Although few are aquatic, most of them live in damp places or are dependent upon an abundant supply of water. From the economic point of view the group is of very minor consequence. To the botanist, however, the bryophytes are of particular interest in helping to picture those ancient plants which first crept out of the sea to invade the dry land, and which therefore took the first steps along the evolutionary road leading up to the now dominant and familiar seed plants.

The bryophytes undoubtedly are a very ancient group and their history is necessarily obscure. There is good reason to believe, however, that they arose from plants resembling some of the higher algae of today, and several connecting links between algae and liverworts have accordingly been suggested. The two main characteristics which distinguish the bryophytes as a whole from these ancestral thallophytes are the establishment of a clearly marked alternation of generations and the possession of multicellular sexual organs.

Alternation of Generations.—As outlined in a previous chapter, these plants possess a definite sexual gamete-producing phase, the *gametophyte*, which is followed in the life history by an equally definite non-sexual, spore-producing one, the *sporophyte*. The sporophyte here is little more than a spore case and is always attached to the tissues of the gametophyte, never becoming an independent individual as it does among the ferns and their allies. The beginnings of this alternation of generations, as has been noted, make their appearance here and there among the

thallophytes, but with the liverworts and mosses it becomes regularly established and henceforth is a distinctive feature in the life histories of all species throughout the plant kingdom.

Multicellular Sexual Organs.—The sexual organs of the bryophytes have also attained a degree of complexity far above those of the thallophytes. In the latter group, with a few minor exceptions, the structures which produce the eggs and the sperms are modified single cells, the gametes being formed directly out of the cell contents. In the bryophytes, however, the gamete-

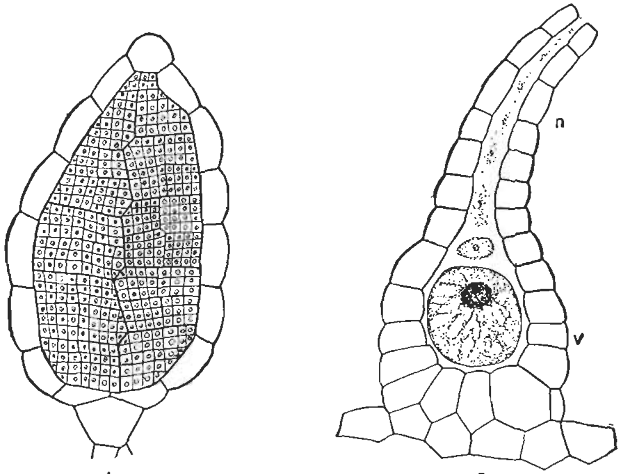


FIG. 204.—Multicellular sexual organs of a bryophyte (*Ricciocarpus*). *A*, antheridium. *B*, archegonium. *v*, venter, *n*, neck. A large egg is evident in the venter, but the ventral canal cell and neck canal cells are largely broken down, following the opening of the neck of the archegonium. See also Figs. 206 and 217.

producing organ has a definite, many-celled wall surrounding the cell or group of cells which develop into the gametes (Fig. 204). The female sex organ is now known as the *archegonium*. It is a somewhat flask-shaped structure, the swollen lower portion of which is termed the *venter* and the elongated upper portion the *neck*. The wall is a single cell-layer in thickness. Most of the cavity of the venter is occupied by a large egg cell, and just above this lies a much smaller *ventral canal cell*. Filling the neck are a row of narrow *neck canal cells*. When wet, the neck opens, the neck canal cells break down, and a sperm enters to fertilize the egg. The male sex organ is still known as the *antheridium*. In bryophytes it has typically a short stalk and is

somewhat elongated. Its wall, one cell-layer in thickness, surrounds a mass of small, squarish cells within each of which a motile sperm is developed, provided with two cilia. When wet, the antheridium breaks open and liberates the sperms, which swim about and under favorable conditions enter archegonia and effect fertilization. Archegonia and antheridia, or structures which have been derived from them, may be recognized in the gametophytes of all the remaining members of the plant kingdom.

Bryophytes are divided into two classes, the *Hepaticae* and the *Musci*.

Hepaticae, or Liverworts.—The members of this class are low-growing plants, chiefly inhabiting moist places. Their

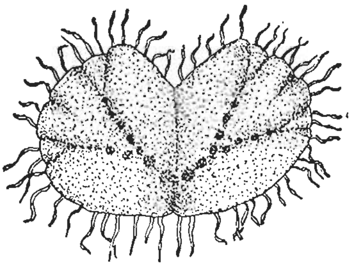


FIG. 205.—*Ricciocarpus*, a simple, floating liverwort. The round bodies lying at the bottoms of the furrows on its surface are sporophytes, each of which has arisen there from a fertilized egg in an archegonium. On the lower surface of the thallus are groups of thread-like absorbing organs or rhizoids.

vegetative body is a flattish thallus which creeps over the surface of the ground, and is attached thereto by thread-like filaments or *rhizoids*. In some types it is cut up into leaf-like lobes. Here are found the lowest and most alga-like of the bryophytes. They are commonly divided into the *Marchantiales*, *Jungermanniales*, and *Anthocerotales*.

Marchantiales.—The thallus of these plants is a thick, dichotomously forking structure, in the upper or dorsal portion of which occur air spaces or chambers, communicating directly with the outside and thus freely exposing to the air the delicate chlorophyll-bearing cells of the interior. It grows in length by the activity of a group of embryonic cells at the tip of each lobe.

In *Riccia* and its allies (Fig. 205), the simplest members of the order, the sex organs (archegonia and antheridia, Figs. 206, *A* and 206 *B*) occur along grooves in the upper portion of the thallus and

are sunken just below its surface. The sporophyte (Fig. 206, *C*) which develops from the fertilized egg is nothing more than a spore case or sporangium, often called among bryophytes the *sporogonium*, and here consists merely of a mass of spores surrounded by a definite wall. These spores, like all produced by sporophytes, occur in groups of four, or *tetrads*. The sporogonium is sunken in the tissues of the thallus, to which it is attached at the base and from which it draws its food.

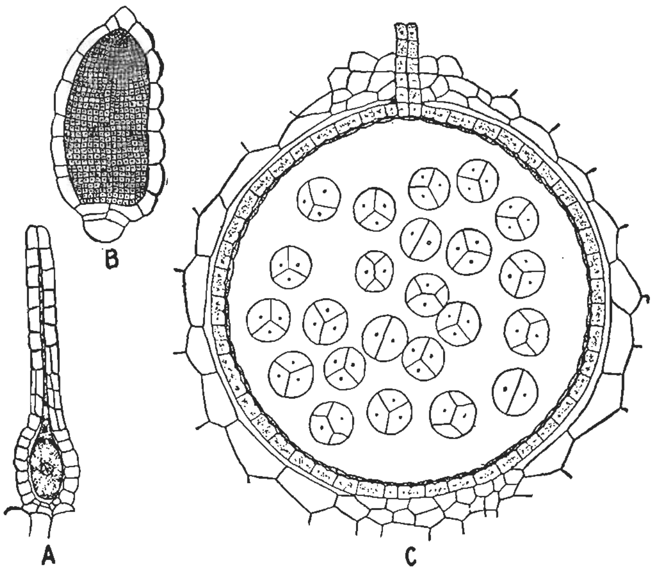


FIG. 206.—*Ricciocarpus natans*. *A*, archegonium. *B*, antheridium. *C*, sporophyte, contained within the remains of the archegonium, and with a thin wall of its own. The spores are borne in groups of four.

In the higher members of the order, as illustrated by the common genus *Marchantia* (Fig. 207), the sexual organs are borne on specialized discs, each carried up above the surface of the thallus by a stalk. The sexes are separate in most species, some gametophytes bearing only antheridia (Fig. 208) and some only archegonia (Fig. 209). The sporophyte (Fig. 210) is more specialized than that of *Riccia* for it includes not only a spore case but a short stalk or *seta*, the growth of which carries the spore case out and away from the thallus. The base of this seta is enlarged into a *foot*, anchoring the sporophyte in the tissue of

the thallus and absorbing food therefrom. Furthermore, not all of the central portion of the sporogonium itself produces spores, for many of the cells grow instead into long, spirally thickened

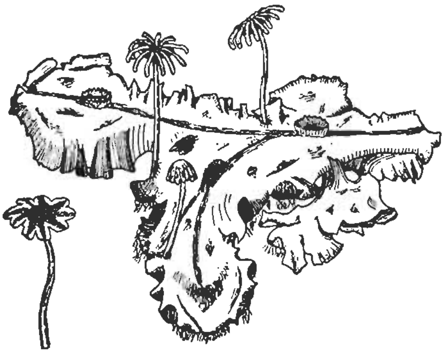


FIG. 207.—*Marchantia.* Thallus bearing female receptacles, in which occur the archegonia. A single male or antheridial receptacle is shown separately.

elements, the *elaters*, which assist in loosening and scattering the spore mass at maturity. The relative amount of sporophyte tissue which does not contribute directly to the production of

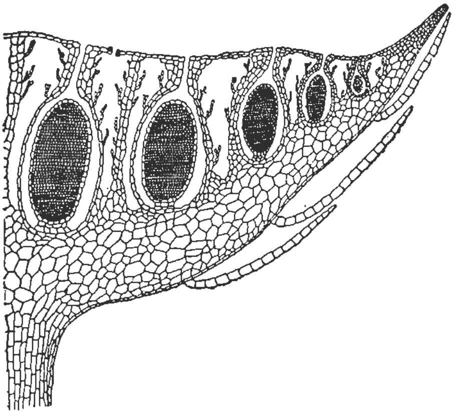


FIG. 208.—*Marchantia.* Section through the male receptacle, showing the antheridia sunken below the surface.

spores, and is therefore called *sterile* tissue, increases steadily during the upward evolution of the sporophyte. In the simplest case (among certain thallophytes), the fertilized egg develops into a group of spores. In *Riccia*, the only sterile tissue is the sporangium wall; in *Marchantia*, the seta and foot are added; in

the mosses still other regions are "sterilized," and in the higher plants the spores themselves constitute but a very small portion of the sporophyte as a whole.

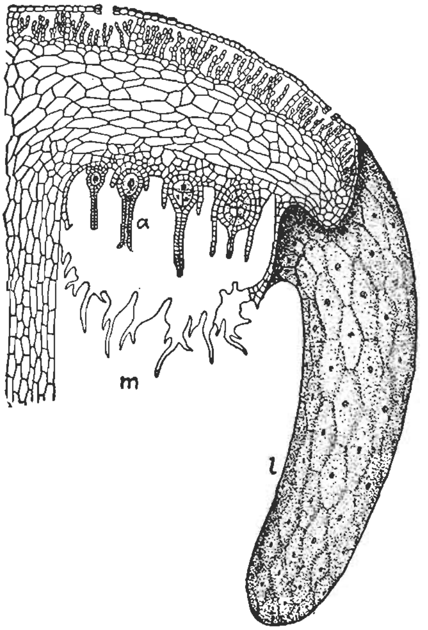


Fig. 209.

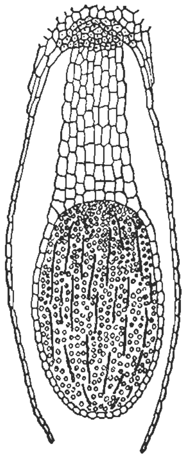


Fig. 210.

Fig. 209.—*Marchantia.* Section through female receptacle. *a*, archegonia, two at left unfertilized, two at right with young sporophytes. *m*, membranous fringe. *l*, finger-like lobe.

Fig. 210.—*Marchantia.* Sporophyte, developed from a fertilized egg. The enlarged capsule contains spores and elaters. It is supported by a stalk or seta, which is imbedded in the tissues of the gametophyte by a foot.

Leafy Liverworts (*Jungermanniales*).—In number of species this order is by far the largest of the three groups of liverworts. Its thallus is much less complex internally than that of the Marchantiales. Externally, however, it is more specialized, for in most species it is divided into a slender axis or stem and three crowded rows of small and delicate lobes or "leaves" (Fig. 211). The stem never rises to an erect position but is always prostrate on the ground, to which it is attached by rhizoids. Sex organs are borne on the main axis or on short lateral branches. The sporophyte develops a much longer seta than in the Marchantiales and the spore case contains still more sterile tissue. At maturity it breaks open into four spreading lobes.

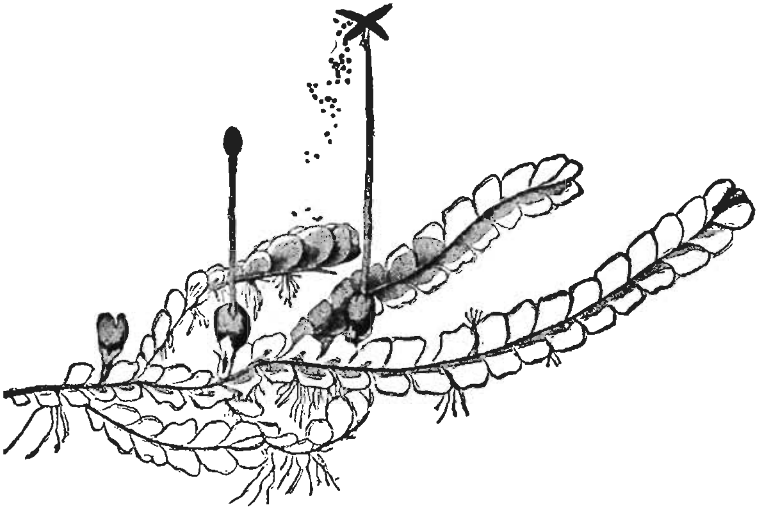


FIG. 211.—A leafy liverwort (*Chiloscyphus*). Portion of the thallus, showing the two rows of leaves and three stages in the development of the capsule. (From *Velenovsky*.)

FIG. 212.—*Anthoceros*. Portion of thallus, showing several sporophytes, one of which is splitting open and liberating the spores.

Anthocerotales.—The gametophyte in this group is a simple, flat thallus (Fig. 212), but the sporophyte is remarkable in

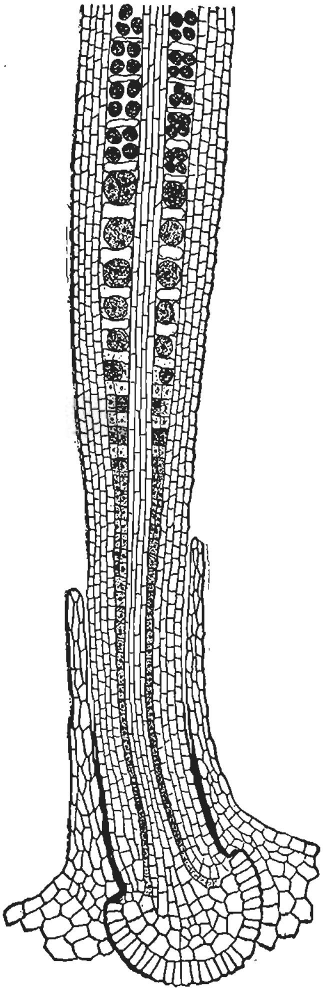


FIG. 213.—The sporophyte of *Anthoceros.* Longitudinal section of basal portion, showing the large foot, embedded in the gametophyte. The spore-bearing tissue surrounds the sterile columella within, and is surrounded by a layer of sterile, chlorophyll-bearing tissue without. The base of the sporophyte continues to grow, adding progressively to these various tissues.

several particulars. In the genus *Anthoceros,* the best known member of the order, the sporophyte (Fig. 213) is long and slender and is well anchored in the thallus by its foot. Just above

the foot is a growing region, through the activity of which the sporophyte continues to elongate during the whole season. The spores at the tip ripen first, and ripening proceeds slowly downward, the spore case gradually splitting into halves (Fig. 212). Its internal structure is more highly differentiated than in any other of the bryophytes. A core of sterile tissue, the *columella*, occupies the center or axis. Around this is a layer of spores, which in many species is broken up by groups of sterile cells. The wall outside this is three or four cell-layers in thickness, and except for the outermost one, or epidermis, its cells are provided with chlorophyll and often are separated somewhat by intercellular air spaces. Well developed stomata, with guard cells much like those in the higher plants, occur in the epidermis. The sporophyte of the Anthocerotales is therefore able to carry on photosynthesis actively, though it still necessarily depends upon the gametophyte for water and mineral salts. This group always has been of particular interest to botanists as suggesting a possible connection between the bryophytes and those higher plants in which the sporophyte has become an independent individual.

Musci, or Mosses.—The mosses are much commoner and more familiar plants than the liverworts, and under certain conditions form an important element in the vegetation. Many of them thrive only in moist situations but others are common on ordinary soil and still others live under xerophytic conditions where few plants can grow. The moss plant is typically erect and consists of a stalk around which small, delicate leaves are arranged in spirals. The stem has very little internal differentiation and the leaves are only one or two cell-layers in thickness, so that the vegetative organs are far from approaching in complexity those of ferns and seed plants. As in the liverworts, the plant is attached to the soil by thread-like rhizoids. The sporophyte also shows an advance over earlier conditions in a progressive increase in sterile tissue, particularly in the higher forms; and in opening by a distinct lid, or *operculum*, at the top.

Two main orders are recognized, the *Sphagnales* and the *Bryales*.

Peat Mosses (*Sphagnales*).—These all belong to the single large genus *Sphagnum*, characteristic of the bogs and swampy regions of temperate climates. The spore germinates into a flat, thallus-like structure from the surface of which arise upright and much

branched shoots, thickly covered with small leaves (Fig. 214). Many of the leaf cells are dead and empty and are so constructed that they will absorb and hold large quantities of water. At the tips of the main branches are borne the sexual organs. The globular capsule is provided with a well developed foot, its wall is thick, and much of the central tissue is sterile, the spores occurring in a rather small, dome-shaped mass in the upper portion. There is no true seta but the sporophyte is carried upward on a stalk formed by the gametophyte.

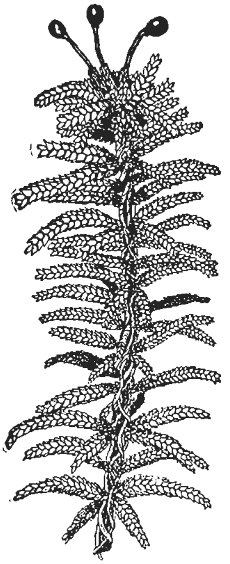


FIG. 214.—*Sphagnum*. Leafy shoot of the gametophyte, with three capsules at the top.

True Mosses (*Bryales*).—These are the common mosses, numbering over 12,000 species and widely distributed over the globe. Many of them are particularly well suited to live in cold or dry situations and they often form the vanguard of an advancing vegetation.

The spore does not germinate directly into the familiar moss plant, but produces instead a mass of green filaments, the *protonema* (Fig. 215). From this arise erect branches which grow into the leafy shoots (Fig. 216). The stem is usually but a few centimeters

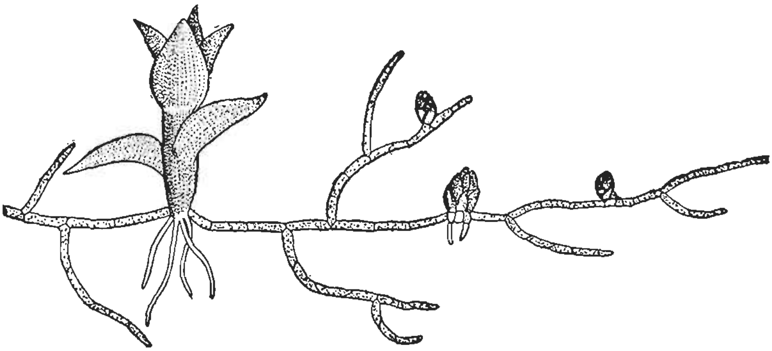


FIG. 215.—Moss protonema, the delicate, thread-like structure which grows from the germinated moss spore. Along this protonema several young moss plants are arising, the one at the left well started, the other three mere buds.

in height and shows little complexity, although there often may be distinguished a firm central mass of tissue—presumably the

region of conduction—and a softer zone outside. Nothing approaching the highly differentiated stem structure of ferns and seed plants is present, however. The leaves are typically

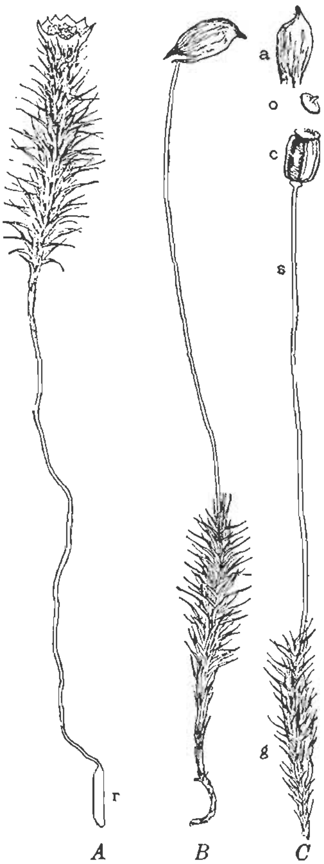


FIG. 216.

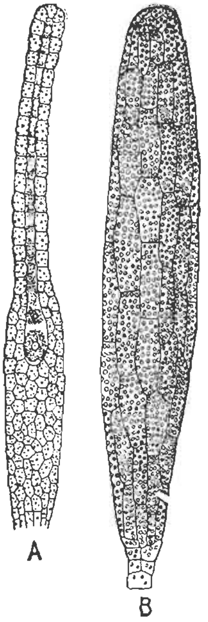


FIG. 217.

FIG. 216.—A moss (*Polytrichum commune*, the hair-cap moss). *A*, male plant which bears antheridia at its tip. *B*, female plant, showing mature sporophyte. *C*, female plant with its various portions separated. *g*, gametophyte or moss plant. *s*, seta or stalk. *c*, capsule. *o*, operculum. *a*, calyptra. (*From Gager's "Fundamentals of Botany," P. Blakiston's Son and Co., Philadelphia.*)

FIG. 217.—Sexual organs of a moss (*Mnium*). *A*, archegonium (in section). *B*, antheridium.

small and narrow, and but one layer of cells in thickness. They often may become very dry and still retain their vitality. The filaments of protonema, to which the moss plant still remains

attached, continue to grow and serve as a means for anchorage, absorption, and dispersal.

Sexual organs (Fig. 217) are borne at the tips of the branches, sometimes on the same plant but often on separate individuals.

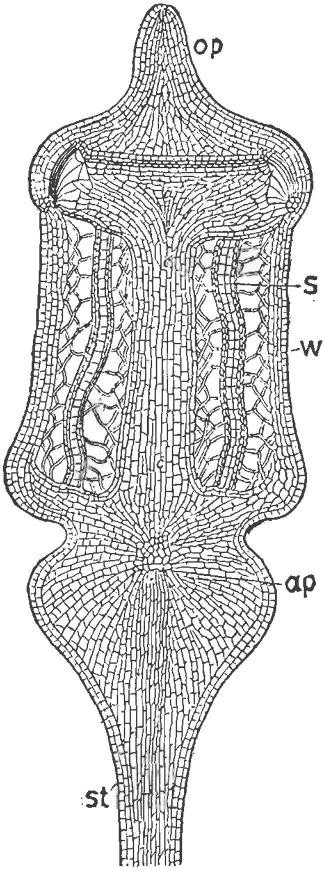


FIG. 218.—Longitudinal section through the capsule of a moss (*Polytrichum*). *st*, seta: *ap*, apophysis; *w*, wall; *c*, columella; *s*, spore sac, surrounded on both sides by loose tissue. (*From Goebel.*)

The sporophyte usually develops a long *seta*, the growth of which carries the capsule far up above the moss plant. Remains of the archegonium are carried up with it and form a protecting cap or *calyptra* which covers the young capsule. The capsule itself (Fig. 218) possesses a central columella and much other sterile tissue, so that the spore-bearing layer, which surrounds the

columella, is relatively thin. The operculum drops off at maturity and the liberation of the spores is controlled by a ring of teeth projecting inward from the edge of the wall. Just below the capsule there is typically an enlarged region, the *apophysis*, which often is brightly colored and may sometimes possess chlorophyll. The capsule is very diverse in size, shape, and structure throughout the whole group.

Fertilization probably is effected rather rarely, owing to the fact that an abundance of water is necessary in which the sperms may swim about. Perhaps as a result of this there occur many devices among the mosses by which asexual reproduction is accomplished, and most of the new individuals produced probably arise by this means.

Despite its large size and relatively high specialization, the mosses are not believed to have led directly to any of the higher plant groups, but botanists look instead to such simpler forms as *Anthoceros* for a suggestion as to how the great gap which now exists between bryophytes and pteridophytes may have been bridged.

QUESTIONS FOR THOUGHT AND DISCUSSION

674. What is the advantage of a multicellular sexual organ over the primitive unicellular type?

675. What reason can you suggest for the presence of the ventral canal cells and the neck canal cells in the archegonium?

676. What exceptions are there to the general rule that the thallophytes have unicellular sexual organs?

677. How does dichotomous branching differ from the typical method of branching of the higher plants?

678. Of what advantage to the moss plant is the seta?

679. What is the probable reason for the fact that bryophytes have never been able to produce plants of any great height?

680. In bryophytes, what are the respective advantages and disadvantages of the thallus type and of the leafy type of plant body?

681. In the general character of their thallus, what group of algae do the liverworts most resemble?

682. Why is it that the liverworts are largely confined to moist places whereas the mosses often thrive in relatively dry ones?

683. What notable resemblance is there in structure between the thallus of the liverworts and the leaves of the higher plants?

684. In what particulars are the Anthocerotales closer to the higher plants than are the rest of the bryophytes?

685. In what respects does the sporophyte of *Anthoceros* resemble and differ from that of the pteridophytes?

686. What changes in the sporophyte of *Anthoceros* would be necessary to make it an independent plant?

687. The shoots of *Sphagnum* are greenish or grayish-green, instead of dark green as in the mosses. Explain.

688. Why is sphagnum (the dead and dried remains of *Sphagnum* plants) an excellent absorbent?

689. What important part in the economy of nature is played by the mosses?

690. What does a moss protonema resemble, and what does its presence suggest as to the ancestry of the mosses?

691. Bryophytes are generally very tolerant of shade. Explain.

692. Where at present on the earth is vegetation headed by a vanguard of mosses?

693. From your study of the bryophytes (and of other plant groups) do you think that all the structures of a plant undergo progressive evolutionary change at the same rate? Explain and illustrate.

REFERENCE PROBLEMS

195. Name as many bryophytes as you can which are of direct economic importance.

196. What are the important structural characters most used in the classification and identification of mosses?

197. Where does peat come from, how has it been formed, and what are its uses?

198. Give the author and title of three important books dealing with bryophytes, and outline briefly the content of each.

199. Name several botanical investigators who have done important work on the bryophytes, and state the notable contributions of each.

200. Give the derivation of the following terms and explain in what way each is appropriate:

Archegonium	Columella	Hypophysis
Elater	Operculum	Protonema
	Calyptra	

CHAPTER XV

THE PTERIDOPHYTA

In passing from the bryophytes to the pteridophytes, which include the ferns, club mosses, and horsetails, one crosses the widest gap which exists in the continuity of the plant kingdom. Intermediate forms between the liverworts and mosses, on the one hand, and the ferns and their allies on the other, are missing; and although various connecting links may be suggested and plausible evolutionary series reconstructed, the transitional plants themselves have perished long since and we probably shall never know just how the present typical land vegetation had its origin.

The Advance from Bryophytes to Pteridophytes.—In the advance from bryophytes to pteridophytes the relative importance of the two generations has been completely reversed. The sporophyte is no longer an appendage of the gametophyte but is now the dominant and conspicuous generation, and has attained complete independence. The sexual plant still is independent, too, but it is relatively small and insignificant, and from this point onward throughout the vegetable kingdom it suffers a steady and progressive reduction. This shift in evolutionary advance from the gametophyte to the sporophyte marks the completion of that great forward step in the plant kingdom whereby a true land vegetation was evolved. The gametophyte is primarily an aquatic or at least a moisture-loving structure. Even in its highest development among the mosses, where it successfully invades the dry land, it never has been able to produce there a strong and vigorous vegetation. The sporophyte, however, seems early to have solved the problem presented by this radical change in environment, and in the pteridophytes it already has developed a stout, branching, subterranean axis, the *root*, clothed with an abundance of root hairs for absorption; large *leaves* presenting to the sun a relatively thick layer of chlorophyll-bearing tissue, which is well provided with air spaces and is protected by an epidermis in which are typical *stomata;* and a stout *stem* on which

the leaves are lifted high in air and which has made possible the development of a tall and vigorous plant body. This advance in external complexity is paralleled by an equally notable internal one, for instead of the relatively simple structure of the moss plant, there occurs the highly differentiated internal anatomy described in earlier chapters. This is distinguished chiefly by the development of those tissues for support and conduction which are called *fibro-vascular*, and which include the wood and the bast. So distinctive of pteridophytes and seed plants is this type of internal structure that these groups are sometimes known collectively as the *vascular* plants, in distinction from the non-vascular thallophytes and bryophytes.

The remarkable advance in vegetative structures which the pteridophytes display is not paralleled in their methods of reproduction. The gametophytes still form archegonia and antheridia though somewhat smaller and simpler ones than those of the mosses, and motile sperms swim to the archegonia and there effect fertilization. The amount of sterile tissue in the sporophyte has increased enormously, of course, owing to the marked development of vegetative structures, but typical spores are still produced in definite sporangia and scattered abroad just as they are among the mosses. In the higher members of the division, two kinds of spores appear: *microspores*, which give rise to antheridium-producing or male gametophytes; and *megaspores*, which give rise to archegonium-producing or female gametophytes. This condition of *heterospory* foreshadows the evolution of the seed, which distinguishes the last and highest plant group, the seed plants.

Pteridophytes are not very numerous in species nor do they form a very conspicuous part of the earth's vegetation today except in certain moist and warm regions. A study of fossil plants, however, shows that members of this division were much more common in past ages, and indeed that at certain periods they were the most notable element in the plant population. Moreover, they then included many stout, tree-like species. In competition with seed plants, the group soon fell from its dominant position and the few descendants which have survived to the present day are for the most part relatively small and simple plants.

Three classes are recognized among the existing pteridophytes; the *Filicineae* or Ferns, the *Lycopodineae* or Club Mosses, and the

Equisetineae or Horsetails. These are so different from one another that they are sometimes regarded as three distinct divisions, but their many points of resemblance make it perhaps more satisfactory to group them together.

Filicineae, or Ferns.—This class, the largest of the three, includes the most conspicuous and familiar of the pteridophytes. The leaves, here known as *fronds*, are typically large and are often

FIG. 219.—A fern plant, the polypody (*Polypodium vulgare*). This is the sporophyte generation. The stem is a creeping rootstock. On the backs of the leaves are born sori, or clusters of sporangia.

deeply cut and dissected. The spores are all alike, except in the small group of water-ferns where heterospory exists. With a few exceptions, the gametophyte grows on the surface of the soil and is provided with chlorophyll, thus existing as an entirely independent plant. Three orders are recognized, the *Filicales, Ophioglossales,* and *Hydropteridales.*

True Ferns (*Filicales*) (Figs. 219 and 220).—Almost all of the ferns belong here, the other two orders being very small ones. In the common species the stem is much reduced and is prostrate or

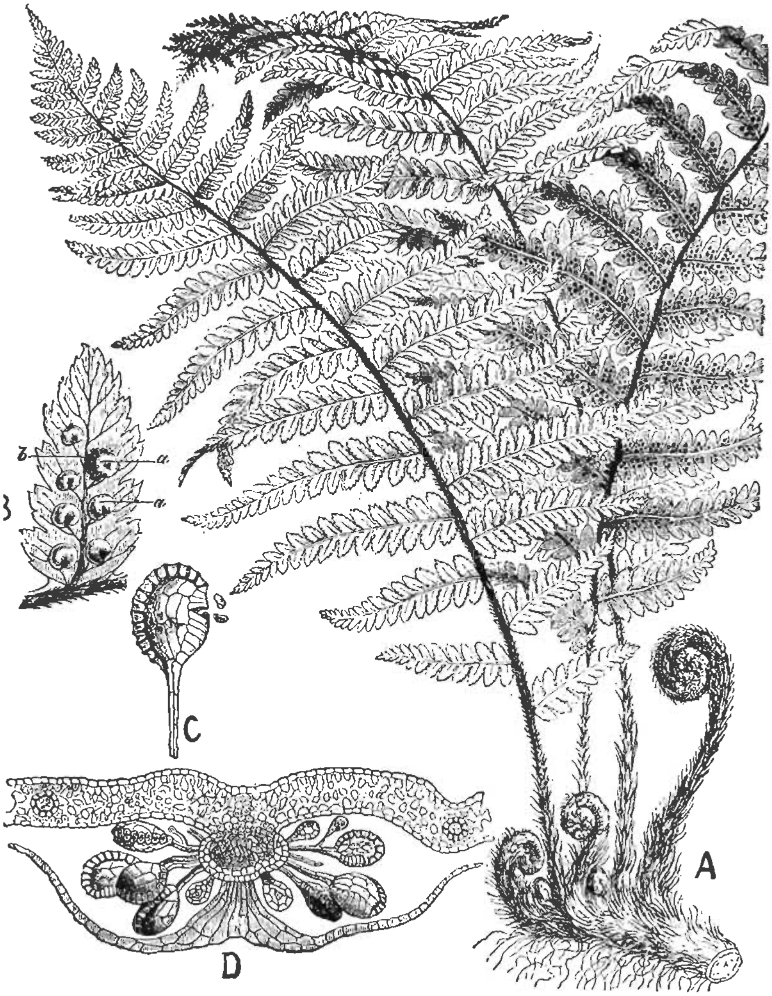


FIG. 220.—The structure of a fern (*Aspidium*). *A*, the plant as a whole. *B*, portion of leaf with seven fruiting dots or sori on its lower surface. Each is covered by an indusium (*a*), from under which the sporangia (*b*) are protruding, in one case. *C*, a single sporangium. *D*, transverse section through a sorus, showing section of leaf blade above and of indusium below, with cluster of sporangia attached between them. (*From Strasburger, after Wossidlo.*)

subterranean, so that the leaves appear to rise directly from the ground. In many tropical types, however, an erect trunk is produced which bears a crown of large leaves at its summit. The fern stem lacks a cambium, and the secondary wood and phloem so common in the seed plants consequently are absent. The fibrovascular system may occasionally be a solid axis, but more commonly is a ring or tube surrounding a central pith (Fig. 221) and is often broken up into a series of separate bundles by gaps, due to the departure of leaves. The phloem here commonly occurs not

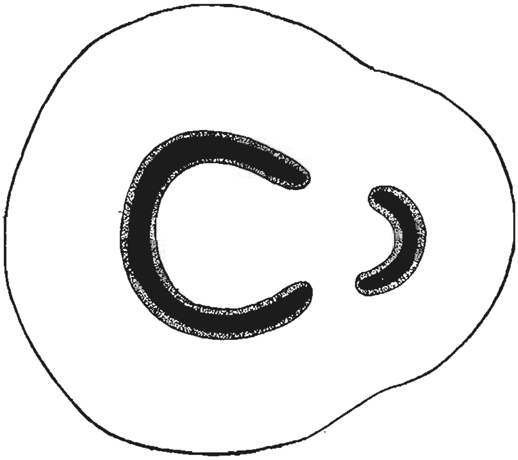


FIG. 221.—Transverse section (diagrammatic) of the stem of a fern (*Adiantum*). The fibrovascular system is here arranged in a hollow tube, the wood surrounded by phloem both within and without. At the right, a segment of the cylinder is passing off to a leaf as a *leaf-trace*, causing a temporary break, or *leaf-gap*, in the cylinder. Wood black, dotted.

only on the outside of the wood but also inside, next the pith, and thus completely surrounds the wood. The cells of both wood and phloem are somewhat less highly specialized than in the seed plants. Particularly in the stouter-stemmed species, the fibrovascular system sometimes becomes very complex and develops several concentric rings of bundles, the members of which are connected with one another in an intricate fashion. Masses of heavy-walled *sclerenchyma* cells are often formed in pith and cortex and aid in maintaining the rigidity of the stem.

The sporangia (Fig. 222) are borne in large numbers on the back or dorsal surface of the leaf in definite clusters (Fig. 220, *B*, *D*)

known as fruiting-dots or *sori* (singular, *sorus*). Each sorus is usually covered until maturity by a fold of thin, skin-like tissue, the *indusium*, which arises from the leaf surface. The individual sporangium is very small in comparison with those of bryophytes and produces only a few spores. In most cases it displays around its wall a characteristic ring of cells, the *annulus*, which is so constructed that upon drying it contracts like a spring, finally rupturing the sporangium wall and forcibly ejecting the spores. The shape and position of the sorus and indusium, as well as the type of annulus, vary greatly among the different groups of ferns and serve as useful characters by which to distinguish genera and families.

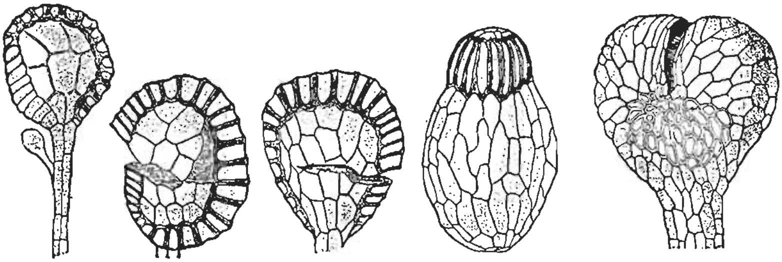


FIG. 222.—Fern sporangia of various types. The ring of heavy-walled cells is the annulus, by the contraction of which the wall of the sporangium is ruptured at maturity and its spores scattered. (*From Strasburger.*)

The spores germinate into a thin, small, thallus-like gametophyte or *prothallus* (Fig. 223) which possesses, chlorophyll and is often somewhat heart-shaped in outline, though its form varies considerably. It is rarely more than a few millimeters in diameter and lies flat upon the surface of the soil, to which it is attached by delicate rhizoids growing from the under surface. Plentiful moisture and a partially shaded situation are necessary for the successful growth of fern prothallia. The sexual organs (Fig. 224), are produced on the under surface, the archegonia near the "notch" (where this is present) and the antheridia farther back, among the rhizoids. The archegonia are much smaller than those of bryophytes and only their necks project above the surrounding tissue. They appear when the prothallus is fully grown and considerably after the antheridia have liberated their sperms. At maturity, the neck of the archegonium opens and the neck-canal cells break down, producing a substance

attractive to the sperms. The antheridium is also very much smaller and simpler than it is among bryophytes. Its wall con-

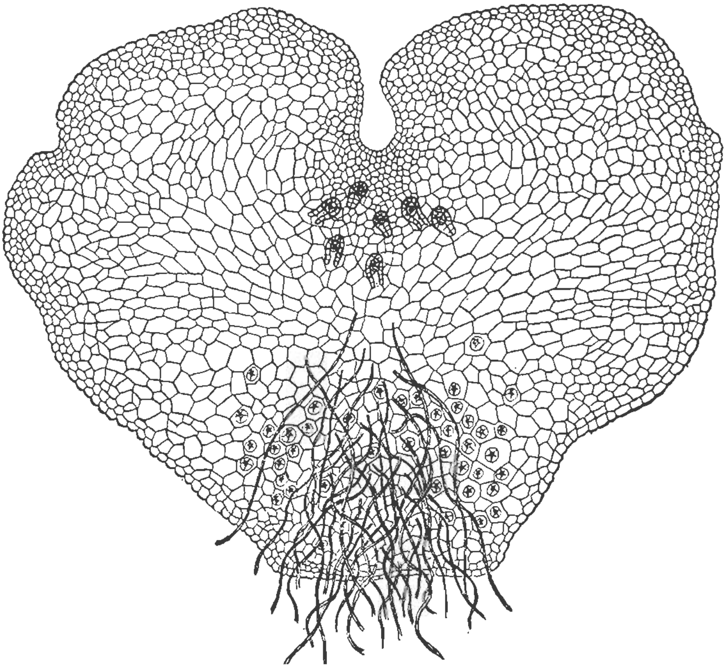


FIG. 223.—The gametophyte of a fern. View of the under surface, which lies next the surface of the ground. Here are borne the archegonia (near the notch) and the antheridia (farther back, among the rhizoids.)

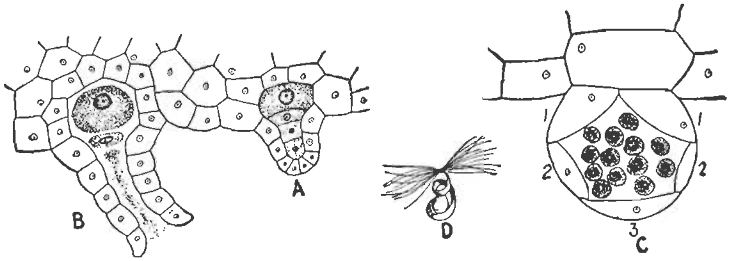


FIG. 224.—Sexual organs of a fern. *A*, section of archegonium just before maturity. Within can be distinguished the large egg cell, below which are the ventral canal cell and two neck-canal cells. In *B*, the archegonium is mature and *its neck has opened. The egg and ventral canal cells are evident*, but the neck-canal cells have broken down. *C*, section of antheridium, showing basal cell (1), ring cell (2), and cap cell (3). *D*, one of the sperms, more highly enlarged.

sists of but three cells—-a cover cell, a circular cell which forms the main wall, and a funnel-shaped basal cell. The contents of the

antheridium divides into a large number of sperms, each possessing a tuft of cilia by which it can swim about in a thin film of water (Fig. 224, *D*). A sperm enters an archegonium and there effects fertilization, after which the fertilized egg, by repeated cell divisions, forms a mass of tissue which gradually becomes differ-

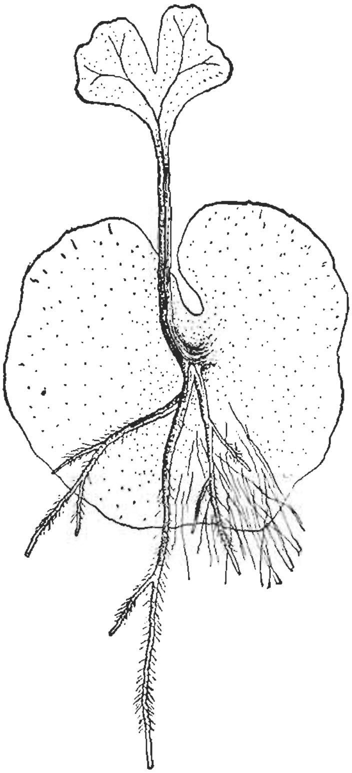


FIG. 225.—Young sporophyte of a fern, which has developed from a fertilized egg, growing out of its parent gametophyte.

entiated into the body of the young sporophyte. A *foot* attaches it to the gametophyte, from which it absorbs food in its early growth. A primary root soon grows downward into the soil and a primary leaf, much smaller and simpler in shape than the mature leaf, rises into the sunlight and the young sporophyte becomes independent (Fig. 225). The gametophyte soon withers and the "sporeling" fern slowly develops into an adult plant and

bears sporangia. The life cycle of a fern is represented graphically in Fig. 226. The order includes about 3000 species and its members are widely distributed over the globe, being particularly rich in species and individuals throughout all tropical regions. It is by far the largest group of pteridophytes and since early times has occupied an important place in the earth's vegetation.

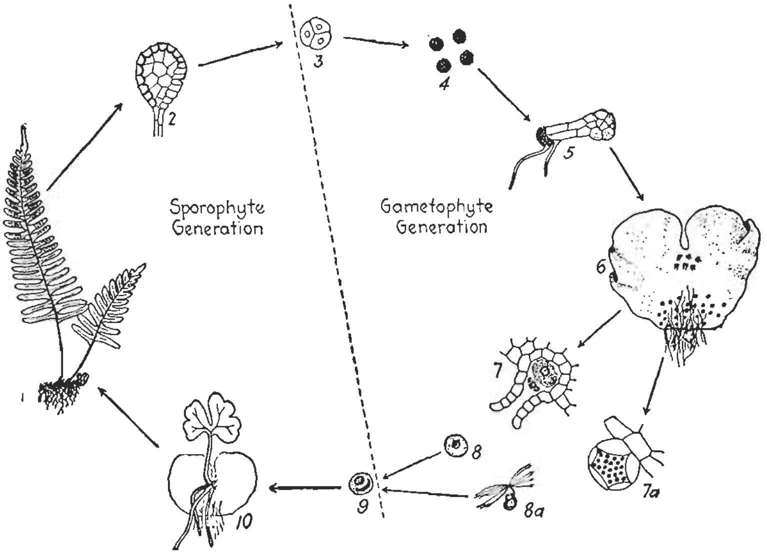


Fig. 226.—Graphic representation of the life-history of a fern. 1, the fern plant or sporophyte, bearing sori, or clusters of sporangia, on its leaves; 2, a sporangium; 3, a tetrad of young spores; 4, the four mature spores which have come from the tetrad shown in 3; 5, a spore germinating into a young gametophyte; 6, mature gameotophyte, bearing sexual organs; 7, archegonium; 7*a*, antheridium; 8, egg cell or female gamete; 8*a*, sperm, or male gamete; 9, fertilized egg; 10, young sporophyte growing out of a fertilized egg, the whole still attached to the remains of the gametophyte.

Adder's Tongues (*Ophioglossales*).—Here are placed a small group of fern-like plants which are of interest to botanists from their possession of certain characteristics markedly different from those of other ferns. A single leaf, simple in the adder's tongue fern (Fig. 227) but typically fern-like in the rest of the order, is produced each season by the subterranean stem. From the petiole of this leaf arises a spore-bearing stalk crowned with a cluster of heavy-walled sporangia, very different in type from the thin-walled structures of true ferns. The gametophyte is

thick and tuberous, and is partly subterranean. The Ophioglossales often are placed by themselves in a separate class.

Water Ferns (Hydropteridales).—This is another small group, chiefly important for its specialized method of reproduction. Its sporophyte is aquatic and bears little resemblance to that of

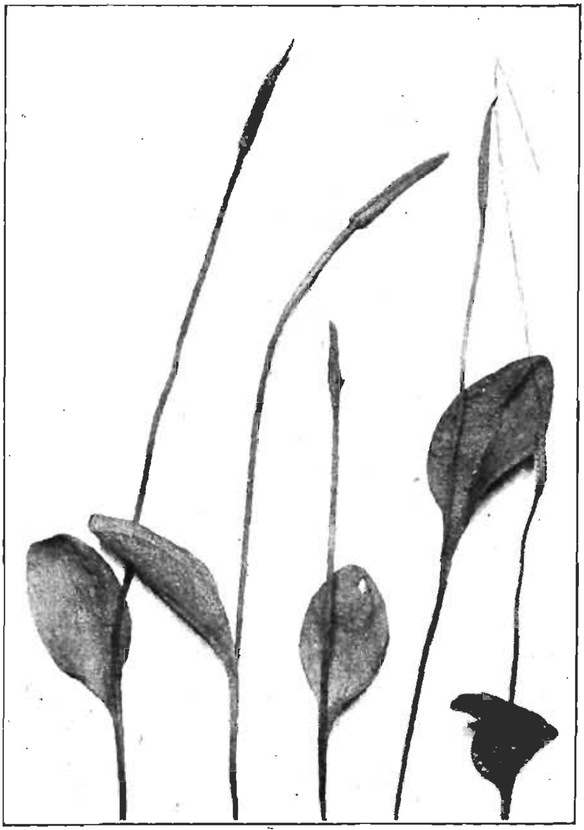


FIG. 227.—The adder's tongue (*Ophioglossum vulgatum*). A group of plants, showing the single leaf and the spore-bearing stalk arising from its surface. (*Courtesy of the New York Botanical Garden.*)

the true ferns. *Marsilia* (Fig. 228), the clover-leaf fern, is the commonest representative. From the petiole of its curious four-lobed leaf arise one or more bean-like *sporocarps* containing sporangia of two sorts: the *megasporangia*, each producing a single large megaspore, and the *microsporangia*, each producing a group of smaller microspores. These are dispersed in the water

and there germinate. The megaspore produces a small female gametophyte still contained largely within the thick spore wall, and at the point where the wall bursts a single archegonium appears. The microspore gives rise to a single antheridium, which liberates into the water a group of sperms. The young sporophyte which develops from the fertilized egg is nourished for a time on the abundant supply of food stored in the female

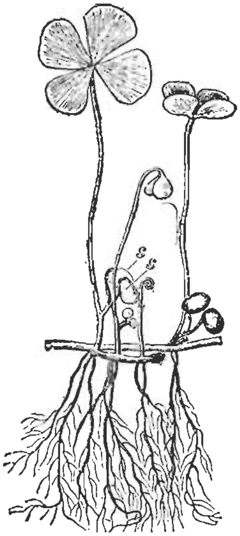


FIG. 228.

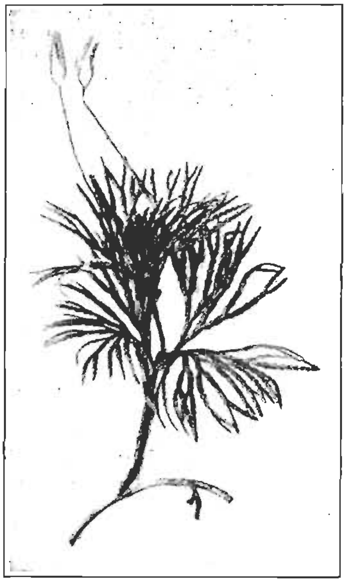


FIG. 229.

FIG. 228.—*Marsilia.* The spore-fruits or sporocarps (*s*) growing out from the petiole of the leaf contain microsporangia and megasporangia. (*From Strasburger, after Bischoff.*)

FIG. 229.—A club moss (*Lycopodium*). The underground stem has sent up a much-branched shoot on which are the small, scale-like leaves. Upon this are borne two groups of cones.

gametophyte, but soon becomes independent through the establishment of a root and leaf of its own. This *heterosporous* type of reproduction is the highest found among the Filicineae.

Lycopodineae, or Club Mosses.—This group is by no means as rich in species as the ferns. The sporophyte (Fig. 229) has a well developed stem, typically prostrate or subterranean but sending up numerous erect branches which sometimes attain a decimeter or more in height. In contrast to the ferns, the leaves are very small, numerous, and crowded closely on the stems,

presenting a moss-like appearance which has given the common name to the group. The internal structure of the stem in *Lycopodium* is unique, for its fibro-vascular system is a solid, pithless core, made up of alternating bands of wood and phloem extending across the central cylinder (Fig. 230). The anatomy of the other genera is much simpler.

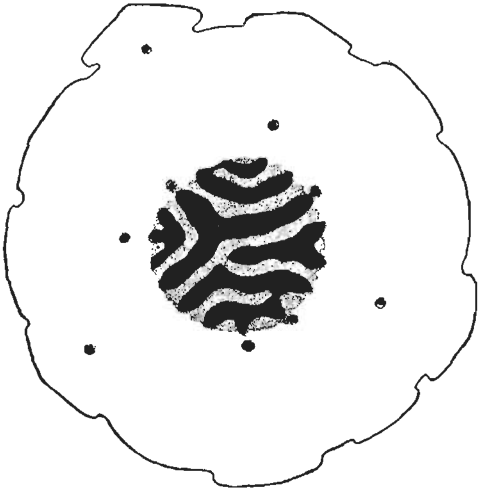


FIG. 230.—Transverse section (diagrammatic) of the stem of *Lycopodium*. The fibro-vascular cylinder consists of alternating bands of wood and phloem. From this cylinder a small leaf-trace departs to each leaf. Wood black, phloem dotted.

Sporangia are few and large as compared with those of the ferns, and are borne on the upper or ventral leaf surface. In the simpler species, a sporangium may arise on an ordinary vegetative leaf but in most cases these spore-bearing leaves (which here, as elsewhere among the higher plants, are known as *sporophylls*) become stout and scale like, and are grouped in a cone or *strobilus* at the tip of a branch. The two main orders, *Lycopodiales* and *Selaginellales*, are distinguished chiefly by their methods of reproduction.

Lycopodiales (Fig. 231).—These are *homosporous* plants, the spores which they produce being all of one sort, as in most Filicales. The gametophytes (Fig. 232) are rarely seen. They vary considerably but tend to develop a stout tuberous, subterranean portion, which may be surmounted by a green aerial

region on which the sexual organs are borne. These are larger and better developed than among the ferns, and the sperms resemble those of bryophytes in being biciliate. After fertilization the young sporophyte is carried rather deeply into the prothallial tissue by a long cell, the *suspensor,* and develops through its early stages largely at the expense of the gametophyte.

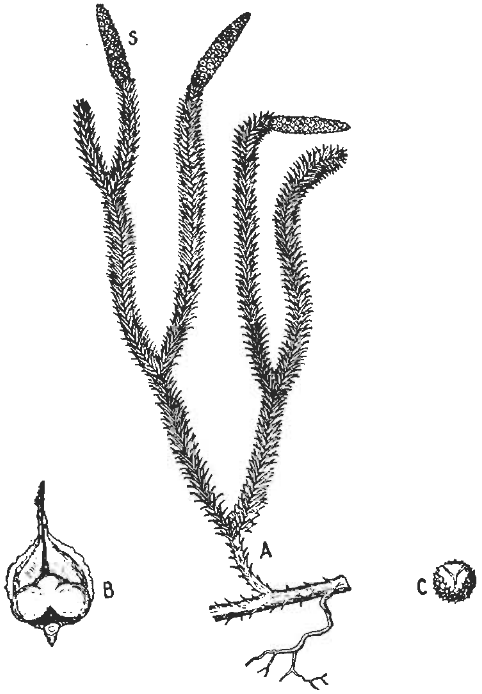


FIG. 231.—*Lycopodium.* *A*, part of a plant of *Lycopodium annotinum* showing prostrate stem and leafy, erect shoots bearing cones or strobili (*s*). *B*, sporophyll or cone scale, bearing a sporangium on its upper surface. *C*, one of the very numerous spores produced in this sporangium, greatly enlarged.

To this order belongs the large genus *Lycopodium,* the familiar club moss or ground pine.

Selaginellales (Fig. 233).—This order is represented by the genus *Selaginella,* which resembles *Lycopodium* rather closely in vegetative structures but differs from that genus in being heterosporous. Certain of the sporangia (the *megasporangia,* Fig. 233, *B*) produce four large *megaspores* each, and the others (the *microsporangia,* Fig. 233, *C*) produce an abundance of much

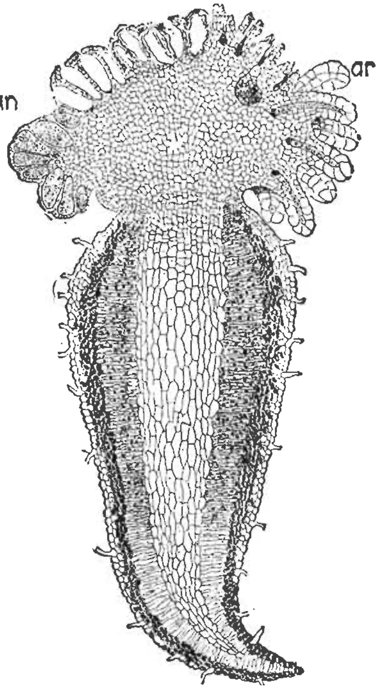


FIG. 232.—Gametophyte of *Lycopodium*, showing the stout, subterranean, tuber-like portion and the upper region in which the antheridia (*an*) and archegonia (*ar*) are produced. (*From Strasburger, after Bruchmann.*)

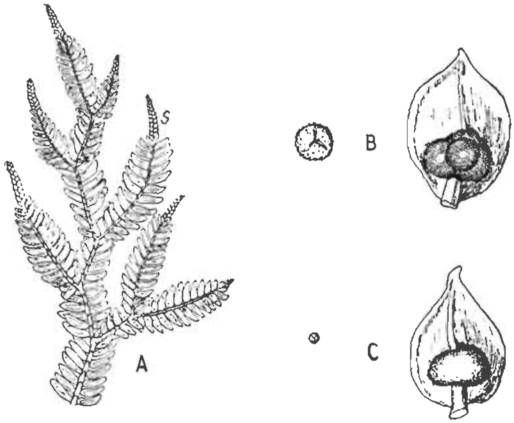


FIG. 233.—*Selaginella*. *A*, leafy branch bearing strobili (*s*). *B*, megasporophyll or cone-scale bearing a megasporangium. One of the four megaspores produced in this sporangium is shown at the left. *C*, microsporophyll or cone-scale bearing a microsporangium. One of the many microspores produced in this sporangium is shown at the left.

smaller *microspores*. The history of the gametophytes is in many ways like that described for the water ferns. The megaspore produces a small mass of cells, most of which are still retained within the remains of the stout megaspore wall (Fig. 234). On the exposed tissue a group of archegonia appear. Each microspore forms a single antheridium in which develops a group of biciliate sperms. The young sporophyte is thrust deeply into the tissues of the gametophyte until it has begun its differentiation. Such a life history as this is clearly a step in the direction of seed production.

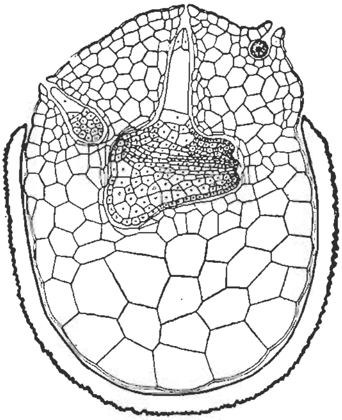


FIG. 234.—Female gametophyte of *Selaginella*. The stout wall of the microspore still encloses part of the gametophyte. At the right is an archegonium; at the center and left, young embryos which have arisen from fertilized eggs in other archegonia. The embryo is carried down into the tissue of the gametophyte by an elongated cell, the *suspensor*. In the larger embryo, the shoot (at right) and root (at left) are beginning to become differentiated, as well as the large, absorbing *foot*, at the lower left. (*Mainly after Pfeffer.*)

The genus *Isoetes*, the quillwort (Fig. 235), is usually included among the lycopods although its remarkable characteristics have caused some botanists to place it in a distinct order. The plants grow in water or very moist places and each consists of a tuft of long, quill-like leaves, arising from a short and flattened stem. In the hollow bases of these leaves the sporangia are borne. *Isoetes* is heterosporous, its gametophytes being similar in general structure to those of *Selaginella* except that the sperms have many cilia.

The lycopods were particularly prominent in the forests of the Coal Period, the great tree-like lepidodendrids and sigillarians

belonging to this order. It is noteworthy that these ancient members of the group possessed a cambium and well developed secondary wood, tissues which are quite absent in living lycopods.

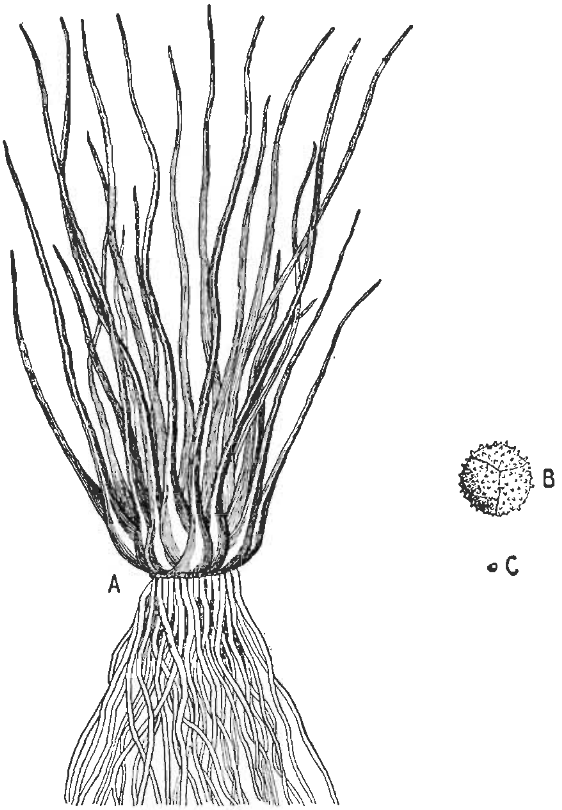


FIG. 235.—*Isoetes.* *A*, general appearance of the plant; *B*, a megaspore; *C*, a microspore.

Equisetineae, or Horsetails.—This very distinct class consists of but one order, the *Equisetales,* and this of but the single genus *Equisetum,* the horsetail or scouring rush (Fig. 236). Some of its species grow in dry sterile soil and others in marshy situations. From a perennial root stock arise the very characteristic stems, which are jointed, ridged, and hollow. Leaves are represented merely by a circle of scales which surround the stem at each joint or node, the green stems carrying on most of the process of photosynthesis. Aside from the large central air space, a smaller one occurs just inside each furrow in the stem (Fig. 237). Oppo-

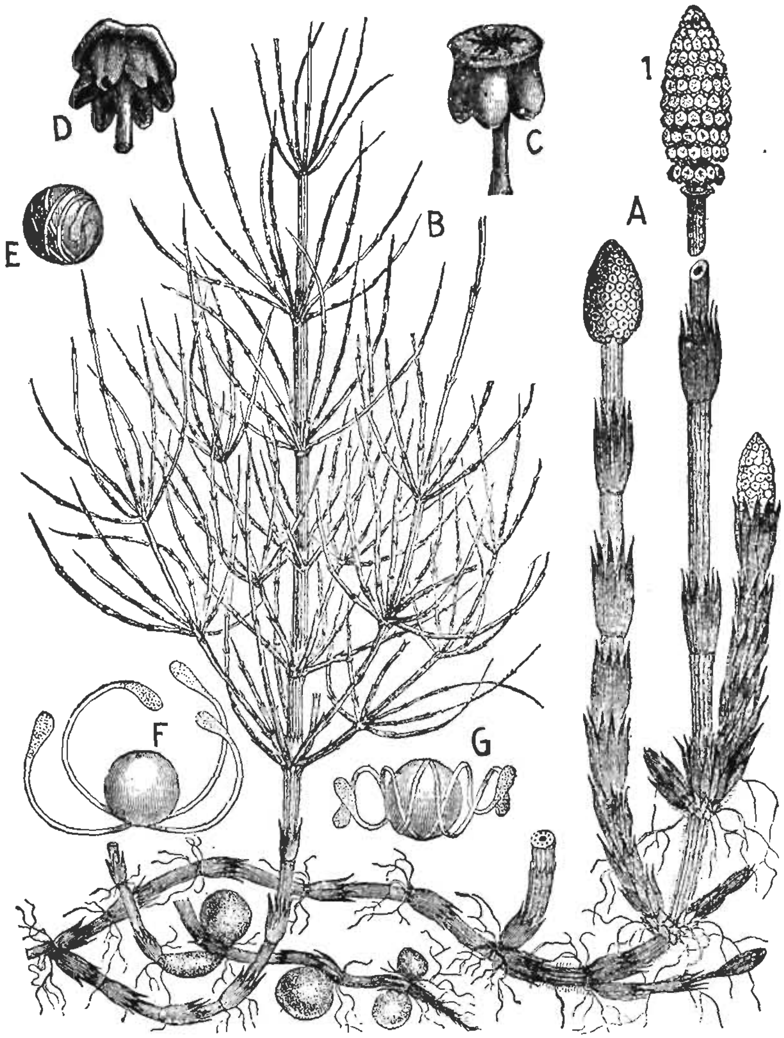


FIG. 236.—*Equisetum arvense.* A plant producing from its underground rootstock several fertile stems (*A*), terminating in cones (1); and a sterile, much-branched shoot *B*. *C*, one of the sporophylls from the cone, bearing a group of sporangia. *D*, the same, with the sporangia ruptured and their spores shed *E*, *F*, and *G*, spores, greatly enlarged, with the elaters in various positions. (*From Strasburger, after Wossidlo.*)

site each ridge is a small and very poorly developed fibro-vascular bundle, the stoutness and strength of the stem being due chiefly to the layers of heavy-walled sclerenchyma which it contains. Across the stem at each node extends a solid partition or diaphragm. The stems may be branched or unbranched.

As in the lycopods, the sporangia are borne in terminal cones (Fig. 236). The sporophylls, however, are not at all leaf-like but are somewhat shield-shaped and project outward at right angles to the cone axis. On their under or inner surfaces are

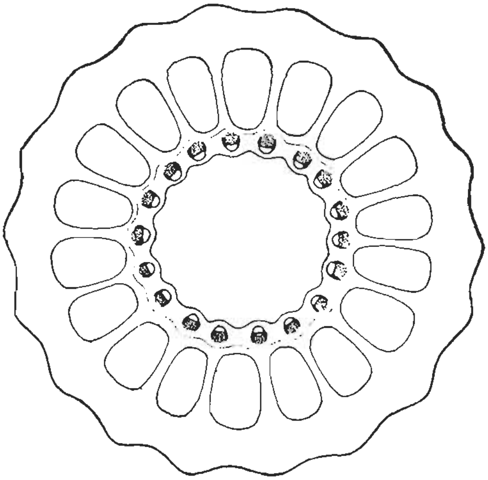


FIG. 237.—Transverse section (diagrammatic) of the stem of *Equisetum*. Note the large central cavity, the air chambers opposite the stem furrows, and the smaller ones in the bundles. The fibro-vascular system is much reduced, consisting of a ring of small bundles, each with two minute arms of wood and a patch of phloem between. Wood black, phloem dotted.

borne a row of sporangia. The spores all are alike externally, but a given spore will generally produce either a male or a female gametophyte. Attached to each spore are four thread-like structures, the *elaters* (Fig. 236, *F*), which coil tightly around it when moist but expand when dry, and thus aid in spore dispersal.

The gametophyte (Fig. 238) is an irregular thallus which develops chlorophyll, shows no tendency toward the subterranean habit of the lycopod prothallus, and is provided with long, branching lobes. The two sexes are usually on separate plants and the gametophytes therefore are said to be dioecious. The sexual organs resemble in general those of other pteridophytes. The antheridia occur at the tips of the lobes and the archegonia

at their bases. Each sperm has a tuft of cilia. In embryonic development no suspensor is formed, and the whole process considerably resembles that found among the ferns.

The Equisetineae, like the Lycopodineae, were represented in earlier periods of the earth's history by large, tree-like species with well developed cambium and secondary wood. Many of these were also heterosporous.

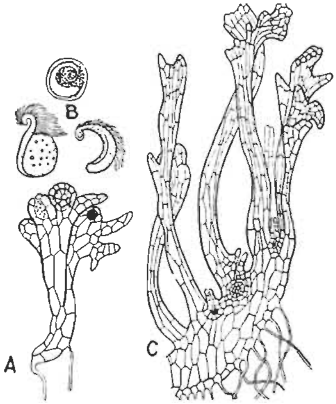


FIG. 238.—Gametophytes of *Equisetum*. *A*, male gametophyte, showing antheridia. *B*, sperms. *C*, female gametophyte, showing the long, branching lobes with archegonia at their bases. (*A and C after Hofmeister, B after Schacht.*)

Chromosome Behavior in the Alternation of Generations.—The alternation of generations was mentioned briefly in describing the life histories of the bryophytes and certain of the thallophytes, but it can be seen most clearly in the pteridophytes, for here the two generations are entirely distinct and each is independent. In plants above the pteridophytes the gametophyte becomes progressively more and more reduced, but the life cycle still shows the same essential features—an asexual generation or phase bearing spores which develop into a sexual generation bearing sex organs, the fertilized egg developing into the asexual generation again. This cycle involves more fundamental differences than those of form and method of reproduction, however. In a previous chapter attention has been called to the importance, in inheritance and development, of those minute constituents of the cell nucleus, the chromosomes, and to the fact that their number is constant within any species. As a result of the union of gametes in fertilization, which ultimately involves the union of their nuclei, the number of chromosomes

must necessarily be doubled, since the nucleus of the fertilized egg contains those of both gametes. If the next generation of gametes, which ultimately are produced by the structure developing from this fertilized egg, should have this same double number of chromosomes, the product of the union of these gametes would have a quadrupled number, and so on. This does not happen, however, for at a point between fertilization and the production of the next generation of gametes there occurs a reduction of the chromosome number to half, through a *reduction division*. In plants showing a typical alternation of generations, this occurs in the cell division *immediately preceding the formation of the spores*, with the result that the double (*diploid*, or $2n$) chromosome number is characteristic of all the cells of the sporophyte generation and lasts from the fertilization of the egg until the production of spores; and that the single (*haploid*, or n) number is characteristic of all the cells of the gametophyte generation and extends from the formation of the spores to the union of the gametes. Thus the sporophyte cells normally have twice the chromosome number of those of the gametophyte, and this criterion is used to delimit accurately the duration of each of these generations.

The details of the reduction division and the points in which it differs from an ordinary body-cell division, are shown in Fig. 239. In the division of the nucleus of the spore mother cells in a sporangium the chromosomes do not split, as in ordinary mitosis, but approach one another very closely *in pairs*. Each pair consists of chromosomes which are similar in size and shape, and presumably in genetic constitution, and they are therefore said to be *homologous*. The two members of each pair now draw apart to opposite poles, and the resulting cells thus contain only half the chromosome number of the mother cells. The two cells thus formed now divide in essentially normal mitotic fashion to form the quartet or *tetrad* of spores with which the gametophyte begins. The diploid number is restored again at fertilization but the two sets of chromosomes (one from each gamete) do not become paired again until the next reduction division; and it is important to note that at this time all the members of one parental set do not go to the same pole but that the two sets may become mixed, some going to one pole and some to the other, thus making possible a mixture and recombination of genetic traits (if the parental types were different) which

results in the production of genetic variability among the offspring.

The relative importance and duration of the two phases of the alternating life cycle is different in the various divisions of the

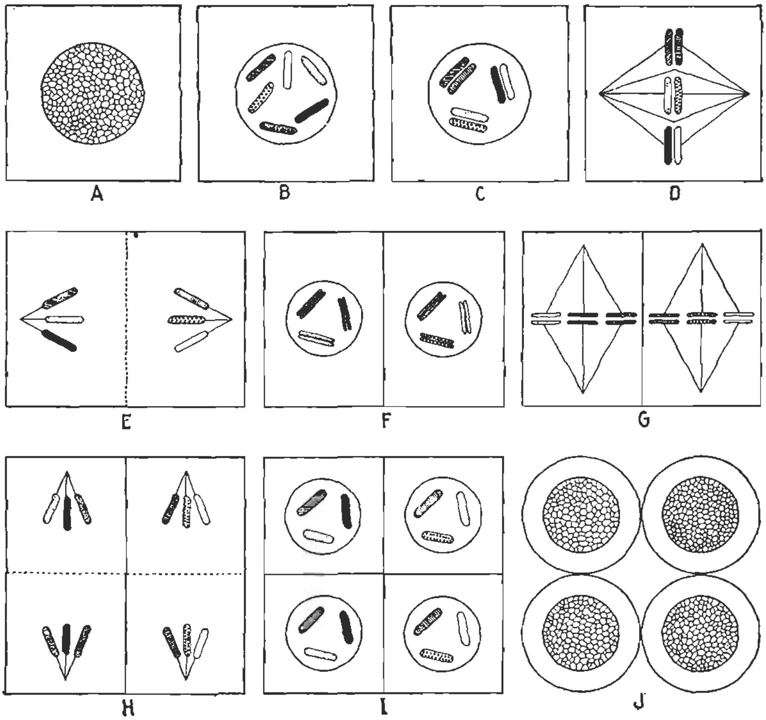


FIG. 239.—Diagram of the "reduction division," which occurs in the development of reproductive cells. Formation of a tetrad or group of four pollen grains. *A*, resting nucleus in the pollen mother cell. *B*, the six chromosomes become distinct, each with an individuality of its own. *C*, these chromosomes group themselves into three pairs. *D*, the three pairs become arranged across the equator of the cell. *E*, the members of these pairs separate, three going to one pole and three to the other. *F*, two new cells are formed, each of which has just half the chromosome content of the mother cell, as a result of this reduction division. *G*, *H*, and *I*: these cells each divide in two normally, producing four cells each with the reduced chromosome number. *J*, four pollen grains which have thus arisen from the pollen mother cell. Compare this figure with Fig. 78. (*Modified from Sharp.*)

plant kingdom, but in bryophytes, pteridophytes, and seed plants the limits between the diploid sporophyte and the haploid gametophyte are distinct and as outlined above. In the thallophytes, however, conditions are not so simple. In some cases the diploid state is present only in the fertilized egg, the reduction

division ensuing immediately so that there is no sporophyte generation. In others practically the entire organism is diploid, as is the case in animals, the reduction division immediately preceding the formation of gametes, and the entire gametophyte generation thus being absent. In still others, both generations are well developed, though they may be externally similar or quite distinct. It is evident that a cytological study of the alternation of generations has placed this rather complex phenomenon in the life history of plants on a much clearer and more logical foundation than is made possible by a study of the external morphology alone.

QUESTIONS FOR THOUGHT AND DISCUSSION

694. Which of the three groups of pteridophytes is the most ancient, in your opinion? Give reasons for your answer.

695. What explanation have you for the fact that the pteridophytes, once the dominant land vegetation of the earth, now constitute such an unimportant part of it?

696. What other groups of plants already described (aside from the pteridophytes) were once probably very abundant but are now represented by only a comparatively small number of species?

697. Why is asexual reproduction so common among the pteridophytes as compared with the seed plants?

698. Do you think that heterospory has arisen more than once in the evolution of the plant kingdom? Explain.

699. Which do you think is more primitive among pteridophytes, thin-walled sporangia or thick-walled ones? Explain.

700. What reasons can you suggest for the fact that ferns are now so much more abundant than club mosses or horse-tails?

701. Why are there no tree-ferns in temperate climates?

702. Why does not the trunk of a tree fern make good lumber?

703. To what, in a bryophyte, does the fern plant correspond? To what does the prothallus correspond?

704. Are common ferns annuals or perennials? Explain.

705. Of what advantage to the fern plant is the indusium?

706. Of what advantage is it to the fern plant to have the archegonia and the antheridia, when on the same gametophyte, mature at different times?

707. In what particulars do the Ophioglossales resemble the ferns? In what do they resemble the club mosses?

708. Do you think that a cone is more, or less, primitive than a group of leaf-like sporophylls? Explain.

709. Of what advantage to the plant is it to have its sporophylls grouped into a cone rather than scattered along the stem?

710. How do a typical fern and a typical club moss differ in the environment to which they are best adapted?

711. What indication is presented by the internal structure of the stem of *Equisetum* as to the type of environment for which this group of plants was originally adapted?

712. What are the advantages of a subterranean, saprophytic gametophyte over the free-living one characteristic of most ferns? Which form do you regard as the more primitive? Explain.

713. In what particulars does *Isoetes* resemble the ferns? In what does it resemble the club mosses?

714. In what particulars do the Equisetales resemble the Filicales? In what do they resemble the Lycopodiales?

715. Of what significance is the fact that the gametophytes of *Equisetum* are usually dioecious?

716. Sometimes a young fern plant develops from a gametophyte by vegetative budding, without any sexual fusion. How many chromosomes (as compared with the n or haploid number for the species) would you expect such a fern plant to have?

717. Sometimes a prothallus is developed as a vegetative outgrowth from a fern leaf. How many chromosomes would you expect a fern sporophyte to have which developed (through fertilization) from such a prothallus?

REFERENCE PROBLEMS

201. Of what economic importance are the pteridophytes

202. Construct for *Lycopodium* a graphic life cycle similar to that given in the text for a fern (Fig. 226).

203. Construct a similar graphic life cycle for *Selaginella*.

204. Construct a similar graphic life cycle for *Equisetum*.

205. Describe the genus *Phylloglossum*, giving its relationships and explaining its particular botanical importance.

206. Describe briefly the plants belonging to the order Psilotales, stating their present distribution and probable relationships.

207. Give an account of some important fossil pteridophytes, describing their structure, geological history, and relationships to living plants.

208. Name some common ferns in which the sporangia are borne on specially modified leaves which have lost their photosynthetic function.

209. Define *apogamy* and *apospory*, and give an example of each.

210. Give the haploid and the diploid chromosome number for five plant species.

211. Just where in the life cycle does chromosome reduction occur in the brown algae? in the red algae?

212. What is meant by a *tetraploid* condition in plant cells? Give some examples of tetraploid plants.

213. Give the author and title of three important books dealing wholly or mainly with pteridophytes, and outline briefly the content of each.

214. Name several botanical investigators who have done important work on the pteridophytes, and state the notable contributions made by each.

215. Give the derivations of the following terms and explain in what way each is appropriate:

Heterosporous	Indusium	Prothallus
Sorus	Annulus	Sporophyll
	Strobilus	

CHAPTER XVI

THE SPERMATOPHYTA

This enormous group, to which the early portions of the text were largely devoted, includes the most familiar and abundant part of the earth's plant population. Directly or indirectly, the seed plants furnish almost all the food supply of the human race, all of its timber and fiber plants, and a great majority of the animal and vegetable products which form the basis of modern civilization. It is this division of the plant kingdom which is present most intimately in the thoughts and lives of men, and which for a long time provided most of the subject matter for the science of botany.

In vegetative characters the spermatophytes are not remarkably different from the pteridophytes. They display the same vigorous development of root, stem, and leaf; and although they commonly show a greater specialization and differentiation of their tissues, particularly in the higher groups, the fundamental plan established in the ferns, with its emphasis on a well developed fibro-vascular system, is retained and further developed. Growth of this system in diameter by means of an active cambium occurs in most seed plants, although it is much reduced or absent in the more delicate herbaceous species.

The Origin of the Seed.—The distinguishing feature of the spermatophytes, as their name indicates, is the development among them of a new reproductive structure, the *seed*. In an earlier chapter there has been outlined briefly the evolution of the seed habit and its significance; but it will perhaps be worth while at this point to describe the seed and its origin somewhat more fully before discussing in detail the various plant groups in which this structure occurs.

Relation to Structures in the Lower Groups.—The seed-producing habit is a direct development from such a condition of heterospory as has been attained by the higher pteridophytes. It will be remembered that in the water ferns, in *Selaginella*, and in *Isoetes*, the spores are not uniform, but that microspores and

megaspores, borne in separate sporangia and on separate sporophylls, germinate into male and female gametophytes, respectively. The seed plants likewise are heterosporous. As in the lower groups, they develop microspores (now called *pollen grains*). These are borne in a microsporophyll (now called a *stamen*). No very radical change is evident here, but in the case of the female structures there are some marked innovations.

The Ovule and Its Contents (Figs. 240 and 255).—The megasporangium, now known as the *nucellus*, produces only one functioning megaspore, for the other three members of the tetrad which begin to develop soon disappear. Furthermore, the sporangium does not burst and liberate this spore but retains it, instead, and *allows it to germinate and produce the female gametophyte within the tissues of the sporangium* (or nucellus), nourished by the parent sporophyte. The female gametophyte (now called the *embryo sac*) is a small, roundish group of cells filled with food and bearing at one end one or more archegonia, or structures comparable to them. The whole is imbedded in the tissue of the nucellus and is never freely exposed. Among the highest forms it suffers such reduction that resemblance to a gametophyte becomes very slight. The nucellus and its enclosed embryo sac are completely surrounded and protected by one or two coats or *integuments* except for a small opening, the *micropyle*, which occurs just opposite the point where the archegonia are borne in the embryo sac beneath. The whole structure—integument, nucellus, and embryo sac—is known as the *ovule*, and after fertilization, for which it is now prepared, the ovule will develop into a seed. It is closely attached to the megasporophyll, which is now called a *carpel*.

Pollen (Fig. 241).—The microspore or pollen grain, produced in the microsporangium, in the meantime germinates and produces within itself the male gametophyte. This is greatly reduced and consists at most of a very few cells, in the higher forms of only two—the generative cell and the tube nucleus. These are all that remain of the male sexual generation. Germination of the microspore usually takes place, at least in part, before it is liberated by the breaking open of the anther wall. After this event, the pollen grain is transferred, by wind, insects, or other means, either directly to the ovule or to a receptive structure (the *stigma*) which is near by. Since the egg cells are buried in the nucellar tissue, it is evident that the male gametes

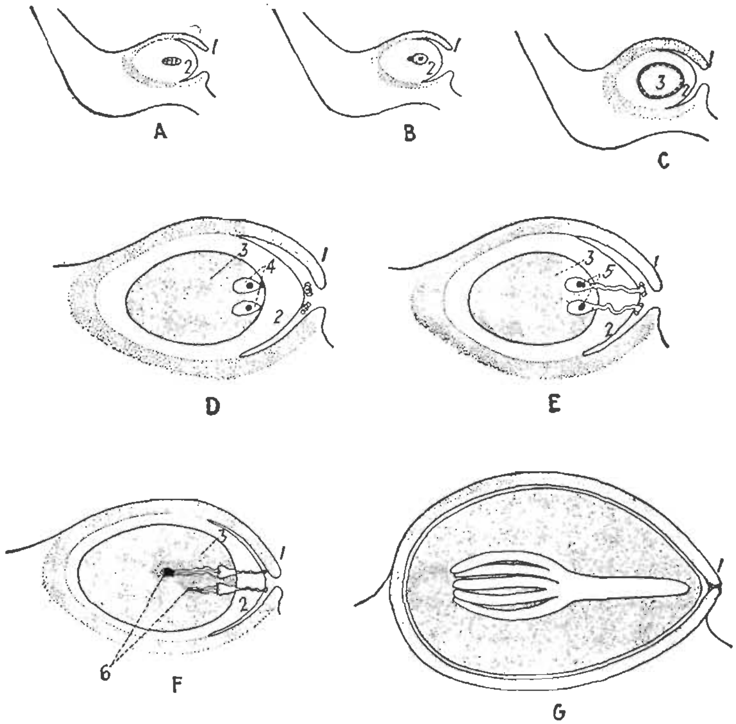


FIG. 240.- Development of the female gametophyte and seed in a gymnosperm (pine). Longitudinal sections through the base of the cone scale. *A*, young ovule, consisting of an integument (1) and a megasporangium or nucellus (2), within which is a row of four megaspores which have developed from a megaspore mother cell. *B*, three of the megaspores have aborted, the fourth is enlarging. *C*, the megaspore has germinated into a young gametophyte or embryo sac (3), which now consists of a layer of free nuclei surrounding a large vacuole. *D*, the young sac has developed into the mature female gametophyte (3), the bulk of which consists of endosperm. At one end are two archegonia (4) within each of which is an egg cell. Pollen grains have entered the micropyle and alighted on the tip of the nucellus. *E*, fertilization. Two pollen grains have germinated, sent their tubes down through the nucellus, and discharged their contents into the two archegonia, in each of which one of the male nuclei is fusing with the egg nucleus (5). *F*, from the fertilized egg have grown two young embryos (6), one larger than the other, which have been pushed down into the middle of the endosperm. *G*, mature seed. The integument of the ovule has developed into the seed coat, the micropyle has closed, the endosperm has become greatly enlargedf the nucellus has almost disappeared and the embryo has grown to its full size, The smaller embryo in *F* failed to develop. (This seed will now detach itsel. from the cone scale and under favorable conditions will produce a new plant.)

cannot approach them directly, as in the lower plants, and a ne\ structure has accordingly been developed which conveys ther to the egg. This is the *pollen tube.* It arises from the polle grain as a slender, thin-walled projection and into it passes th contents of the grain, led by the tube nucleus.

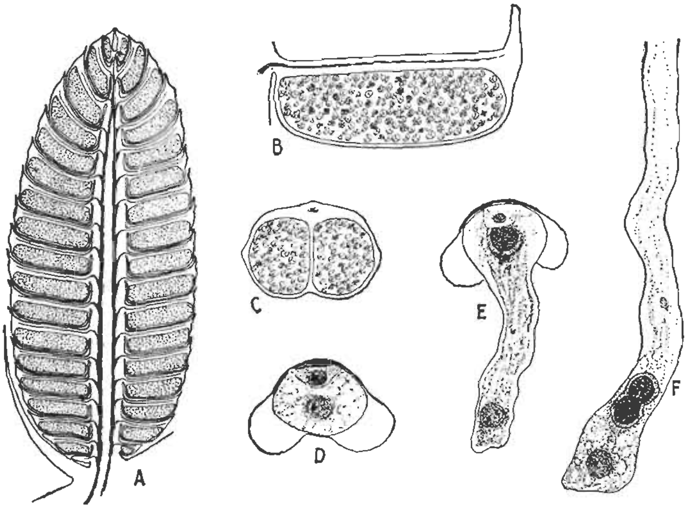


FIG. 241.—Development of the male gametophyte in a gymnosperm (pine *A*, longitudinal section (diagrammatic) of a staminate or "male" cone. *B*, or of the sporophylls from *A*, much enlarged. The sporangium is filled with micr spores or pollen, in various stages of development. *C*, section across the spor phyll at right angles to that in *B*, showing the two sporangia which are borne o each sporophyll. *D*, a mature pollen grain. The outer wall (in the case of pir pollen) is puffed out somewhat at two points, forming balloon-like "wings which add to the buoyancy of the grain. The single nucleus of the megaspoı has now divided to form the *generative cell*, *lying next the wall*, and the tuk nucleus, in the center of the cell. *E*, a germinating pollen grain. The tuk nucleus follows close behind the end of the growing tube. The generative ce has divided into a stalk cell (lighter) and a body cell (darker). *F*, the end of tł pollen tube just before fertilization. The body cell has developed into tł two male cells or gametes, which have now come down the tube and are ready 1 effect fertilization.

Fertilization and Seed-production (Figs. 240 and 255).—Th pollen tube grows rapidly and penetrates the tissues, much as fungus filament penetrates the tissues of its host, until it reache the embryo sac and the egg cells. A large nucleus in the tub often the only one at this point except the tube nucleus, no divides into two male gametes, and as the end of the tube burst into the sac one of these unites with an egg. The fertilized eg now divides and grows into a young sporophyte, the *embry* possessing a primitive root, stem, and leaves. The embry

soon stops its growth and becomes dormant, imbedded in the tissues of the sac which by now are filled with reserve food or *endosperm.* The integument in the meantime has developed into a tough *seed coat* and the whole structure soon separates from the mother plant as a mature *seed.* Under favorable conditions of temperature and moisture this seed will germinate, the embryo breaking out through the seed coats and establishing itself in the soil as a new plant, which grows for a time at the expense of the stored food but soon becomes independent.

The Advances from Pteridophytes to Seed Plants.—The essential advances made by seed plants over the higher pteridophytes are therefore: (1) the retention of the megaspore within the megasporangium and its germination there into the female gametophyte; (2) the enclosure of the sporangium and sac by a new structure, the integument; (3) the transference of the reduced male gametophyte directly to the vicinity of the female gametophyte, to which the male gametes obtain access by another new structure, the pollen tube; (4) the development of the young sporophyte in contact with, and at the expense of, the parent sporophyte; and (5) its final release, dormant, well supplied with food, and protected by a heavy coat. It is noteworthy that the reversal of the reproductive situation as it occurs in the bryophytes is now complete, for instead of the sporophyte being attached to the gametophyte, the gametophyte (and even the succeeding sporophyte) is here attached to the parent sporophyte. Indeed, in the most advanced types both gametophytes are so much reduced that little beside the sexual cells remains, and the alternation of generations has practically disappeared.

The Flower.—The sporophylls of seed plants tend to be arranged in distinct clusters on short branches. In the lower members of the group these clusters are entirely similar to the cones of some of the pteridophytes, but higher up a very specialized shoot, commonly called the *flower,* has been evolved. In its fully developed form this contains not only the stamens and carpels, but modified leaf-like structures for protection of the sexual organs and for attraction of insects. From the possession of this structure the spermatophytes are sometimes called the "flowering plants."

To describe adequately the various orders of which this huge division is composed is quite impossible within the limits of this text. Aside from its numerous and varied living members it also

includes a great number of fossil types, many of which are important in reconstructing the steps in the evolutionary history of the seed plants. Only the salient characters of the more important groups will be presented here, together with their probable relationship to each other and their place in the phylogeny of the whole series.

Gymnospermae, or Gymnosperms.—Two classes of seed plants are commonly recognized, the gymnosperms and the angiosperms, differing chiefly as to the manner in which the ovules are borne. The *gymnosperms are the most ancient of* seed plants, and a varied and heterogeneous group. All agree in possessing ovules and seeds which are borne openly on the megasporophyll or carpel, freely exposed to the air and to the direct contact of pollen grains, and not inclosed in an ovary as they are among the angiosperms. There is good reason to believe that the earliest gymnosperms arose from fern-like ancestors, for several remarkable fossil plants from the Coal Period have been discovered which possessed typically fern-like foliage, and long were thought to be true ferns, but which now are known to have borne undoubted, though primitive, seeds. This group, sometimes called the *Cycadofilicales* or cycad-ferns, has long been extinct, nor have any of its near relatives survived. The most primitive living gymnosperms are the Cycads.

Cycads (*Cycadales*).—Cycad stems are typically stout and unbranched, and bear at the top a crown of large, pinnate leaves (Fig. 242). A few species have tall, columnar trunks and thus superficially resemble tree ferns or palms. Internally, the stem possesses a large pith and cortex but its woody tissue is rather weakly developed, although the fibro-vascular system often is complicated by the occurrence of several concentric rings of bundles instead of a single ring.

The male and female sexual structures occur on separate plants, and the sporophylls are borne in terminal cones (Fig. 243). In the genus *Cycas*, the ovulate sporophylls ("female" cone scales) are large and lobed, showing a slight resemblance to foliage leaves, and bear ovules along their edges (Fig. 244, *A*). In the other members of the order the cones are more compact and the sporophylls or cone scales have lost their leaf-like character. Each microsporophyll (Fig. 244, *B*) bears many sporangia or anthers and produces a large amount of pollen. The ovules are generally large and thick-walled, and the megaspore, arising as

one of four potentially spore-producing cells in the middle of the nucellus, develops into a large embryo sac. At the tip of the nucellus, just under the micropyle, a large, liquid-filled *pollen chamber* forms. The pollen grain enters this chamber through

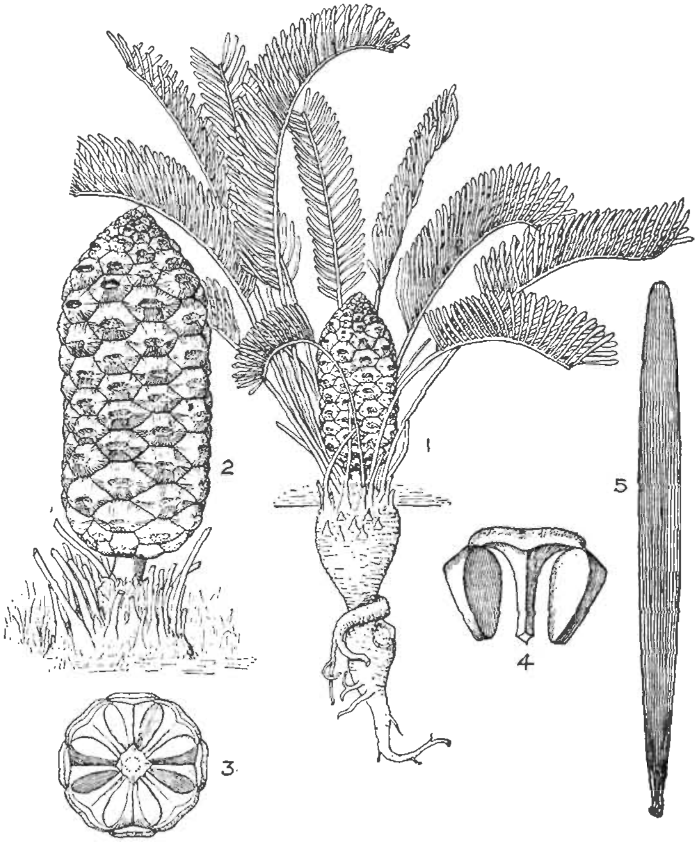


Fig. 242.—One of the Cycadales (*Zamia floridana*). 1, female plant; 2, ovulate cone; 3, cross section of ovulate cone; 4, longitudinal section of ovulate cone scale with ovules attached; 5, leaflet, showing dichotomous venation. (*From Wieland.*)

the micropyle and there germinates. Its two male cells are each provided with a spiral band of cilia (Fig. 245) and swim about in the liquid, a remarkable persistence of the motile habit in male gametes which has survived through pteridophytes and bryophytes from their remote algal ancestry. A pollen tube is formed and penetrates the adjacent nucellar tissue, but it seems rather

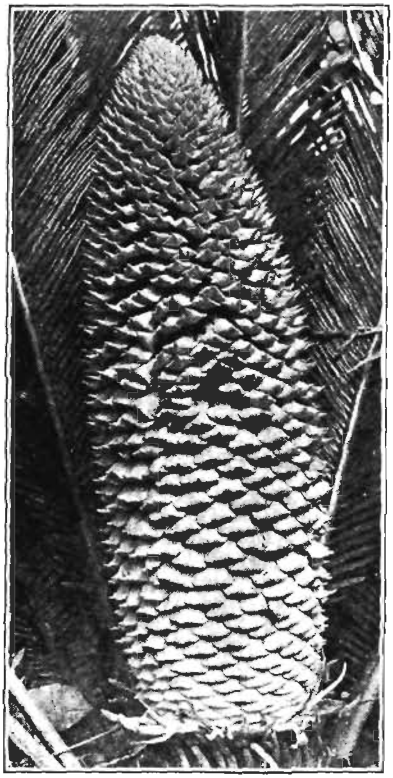
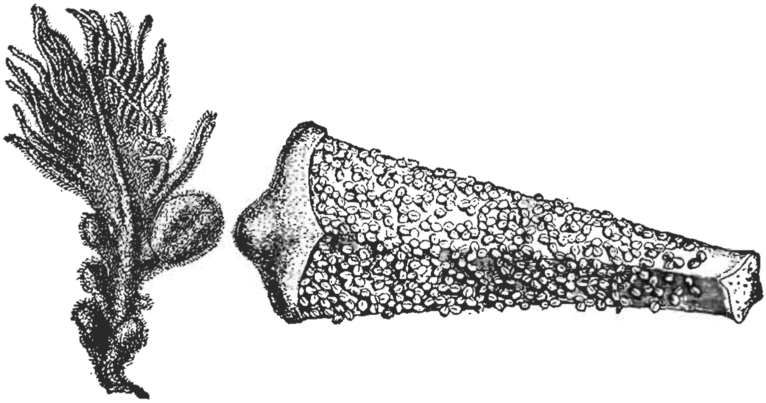


FIG. 243.—Staminate cone of *Cycas revoluta*. (*Photo by G. S. Torrey.*)



A B

FIG. 244.—*Cycas*. At left, sporophyll from ovulate cone, showing several ovules attached to its side. One seed has developed. At right, sporophyll from staminate cone, showing numerous pollen sacs or microsporangia. (*From Strasburger, after Sachs and Richard.*)

FIG. 245.—Cycad pollen tubes entering an ovule, showing the motile sperms. (*From Chamberlain.*)

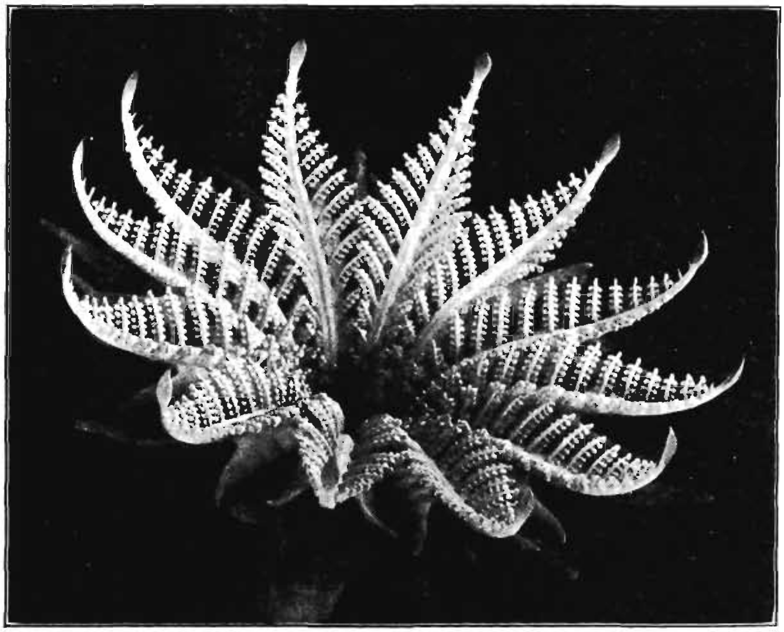


FIG. 246.—Restoration of a "flower" of one of the Bennettitales (*Cycadeoidea ingens*). The complex pinnate structures are the microsporophylls or "stamens" and in the center is the ovulate cone bearing ovules and sterile scales. (*From Wieland.*)

to absorb food than to assist in the transference of the male cells, for the pollen chamber gradually enlarges itself until it reaches the embryo sac, where one of the sperms enters an archegonium and effects fertilization.

Cycads are confined to the warmer regions of the globe. They are an inconspicuous group today but in earlier ages, notably in the Mesozoic period, were abundant and diversified. Their

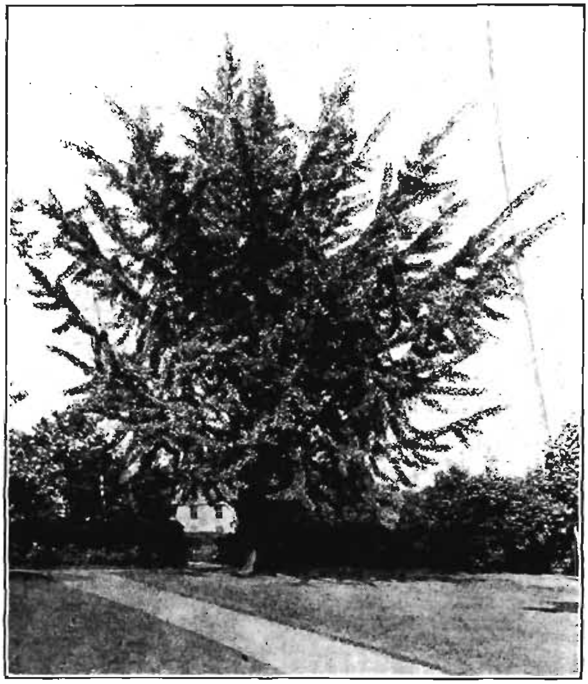


FIG. 247.—*Ginkgo biloba*, the Japanese maiden-hair tree. (*Courtesy of the New York Botanical Garden.*)

close relatives, the *Bennettitales* (now extinct), were for a time among the most conspicuous of plants and produced some complex flower-like bisexual reproductive organs (Fig. 246).

Closely related to the cycads is the Japanese maiden-hair tree, *Ginkgo* (Fig. 247), usually placed in a separate order by itself. It resembles the cycads in the possession of a pollen-chamber and of motile sperms, but differs in its tree-like habit of growth and in the absence of typical cones.

Conifers (*Coniferales*).—These are familiar to everyone from their wide distribution in temperate zones and from the fact that they include many of the most important forest trees. The vegetative body differs radically from that of the cycads for it is usually a tree, with a straight trunk and spreading lateral branches which give a spire-like shape to the whole (Fig. 9). The leaves are typically small, evergreen scales or needles. The bulk of the stout woody stem is secondary wood, laid down by an active cambium. Its water-conducting cells all are tracheids, those produced in the spring being comparatively wide and thin-

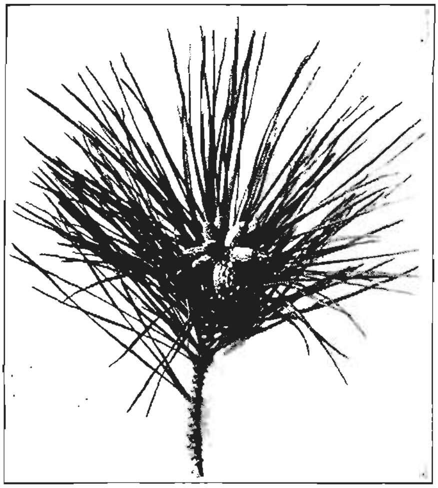


FIG. 248.—Staminate or "male" cones of the pine.

walled and those in the summer much narrower and thicker-walled (Fig. 68). The general structure of the vascular tissues approaches rather closely to that of the angiosperms.

As its name implies, the reproductive structures in this order are produced typically in cones. The microsporangial (staminate or "male") cones (Fig. 248) are short-lived and somewhat delicate structures, and each cone scale (stamen or microsporophyll) bears two (rarely more) microsporangia on its lower or dorsal surface, in which the microspores or pollen grains are developed (Fig. 241). The pollen in all cases is transferred to the ovules by wind. Except for the rather small group Taxineae, in which cone scales or integuments become fleshy at maturity, the megasporangial (ovulate or "female") cones (Figs. 249 and 250) usually

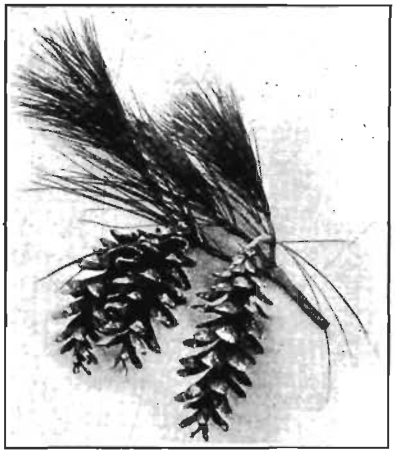


FIG. 249.—Ovulate or "female" cones of the pine.

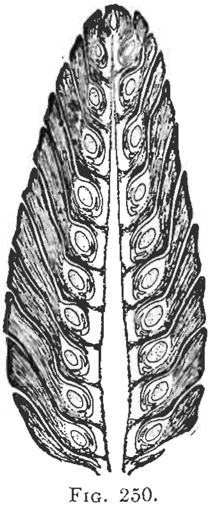


FIG. 250.

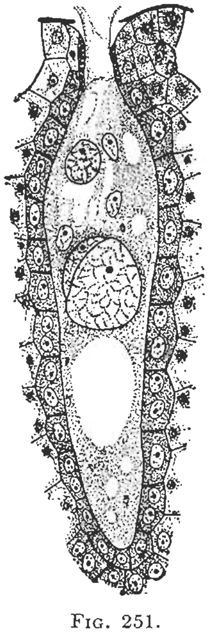


FIG. 251.

FIG. 250.—Longitudinal section (diagrammatic) of the ovulate or "female" cone of pine. Attached to the base of each scale is seen an ovule, its micropyle pointing inward.

FIG. 251.—Fertilization in a conifer. Archegonium into which a pollen-tube has just entered. One of the male nuclei may be seen uniting with the egg nucleus. The other, left behind in the cytoplasm, will die.

become hard and woody. Each cone scale bears one or two ovules. In most cases the embryo sac is distinctly smaller than that of the cycads and contains fewer cells (Fig. 240). The pollen alights on the nucellus and there germinates (Fig. 241). The generative cell at this time divides into two, a *stalk cell* and a *body cell*, which are believed to represent the remains of an antheridium. The body cell in time follows the tube nucleus down the pollen tube and divides into two male cells, one of which effects fertilization (Fig. 251). No pollen chamber is formed, but the pollen tube conveys the male cells, which are non-motile, directly to the archegonia. After fertilization there are a few divisions of the egg within the archegonium itself, and the young *proembryo* thus formed is then carried deeply into the tissues of the embryo sac by certain of its upper cells, which rapidly elongate. In this position it develops into the mature embryo of the seed.

Like cycads, the conifers are an ancient group and are prominent in fossil floras since Mesozoic times. Although they include only about 350 species today, they cannot well be called degenerate, for in many parts of the forested regions of both the north and the south temperate zones they contribute to the vegetation such notable trees as the pines, spruces, firs, larches, hemlocks, cedars, cypresses, and many others.

Gnetales.—Brief mention should be made of the most highly specialized order of gymnosperms, the *Gnetales*, which consist of three genera only: a tropical climber, a desert shrub, and an anomalous desert plant. These are distinguished from other members of the class chiefly by the possession of vessels or ducts in the wood and by a marked reduction in the female gametophyte somewhat similar to that which occurs among angiosperms. It has been suggested that through forms related to the Gnetales, the angiosperms may perhaps have arisen from the gymnosperms.

Angiospermae, or Angiosperms.—Angiosperms differ from gymnosperms chiefly in the fact that their seeds are not directly exposed to the air on the open surface of a scale, dut are enclosed in a definite case or vessel, the *ovary*.

With their 135,000 species, their highly perfected and typically insect-pollinated flowers, their enormously diversified plant bodies, their successful invasion of all habitats, and their assumption of practically every mode of life exhibited by plants, the angiosperms stand at the apex of the vegetable kingdom. They

are a modern group and have arisen in comparatively recent geological time. Before the competition of this new, vigorous, and well-equipped phalanx the older vascular plants have been swept aside, many of them to complete extinction and the rest, with few exceptions, to comparative insignificance. It is only the thallophytes, with their specialization for aquatic, parasitic, and saprophytic habits of life, that can compare with angiosperms in number of species and individuals, and it should be remembered that were it not for these higher seed plants, practically all saprophytes and parasites would perish. The angiosperms are of primary importance as food producers for animals and man.

Since it is the angiosperms which have been studied almost exclusively in the earlier chapters of the text, it will not be necessary to treat them here in as great detail as in the cases of other groups. It will be worth while, however, to bring together the essential features of the class as a whole, that it may be compared readily with the other seed plants and be seen in its proper relation to the rest of the plant kingdom.

Vegetative Structures.—The vegetative body is much diversified. Seed plants not only include trees and smaller woody plants, (the only growth forms displayed by gymnosperms), but they have developed a new type, the *herb*, which is particularly well adapted to temperate or semi-arid regions, since it is small and soft-stemmed, produces flowers and fruit after a very short growing period, and can survive winter, dry seasons, and other unfavorable periods either underground or in the form of resistant seeds. In perennial herbs the underground parts survive and it is only the upper portions which die back; in biennial herbs, the plant lives through two seasons, storing up food the first and flowering the second; and in annual herbs the plant body lives through only one season, and survives unfavorable conditions in the seed. Herbs now are very rich in species and include the majority of food plants and many others of economic importance.

Internally, the vascular system reaches in angiosperms its highest degree of specialization. A cambium is well developed in the woody members but is much reduced among herbs. The wood consists not only of those general-utility elements, the tracheids, but also of thick-walled *fibers* whose function is to furnish rigidity to the stem; and of wide, thin-walled *ducts* or *vessels*, by which large quantities of water can be conveyed rapidly through the wood. In the phloem, too, a new element,

the *companion cell*, intimately related to the sieve tube, makes its appearance.

Reproduction.—The gymnosperms are all wind-pollinated, and many of the lower angiosperms resemble them in this respect and have inconspicuous, cone-like reproductive organs (Fig. 122). The higher members, however, have come to depend upon insects to transport their pollen, and have evolved the characteristic *flower* (Fig. 252) which has been described in a previous chapter,

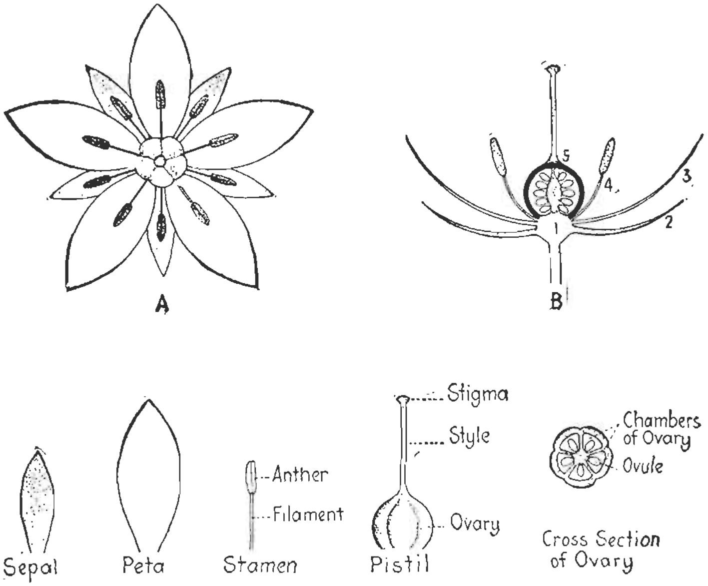


FIG. 252.—The structure of the flower of a dicotyledonous seed-plant (diagrammatic). *A*, face view of the flower, showing its calyx of five sepals, its corolla of five petals, its ten stamens and its pistil. *B*, longitudinal section, showing the relations between the parts. 1, receptacle. 2, calyx. 3, corolla. 4, stamen. 5, pistil, with ovary cut lengthwise.

with its protective calyx, composed of sepals; its attractive corolla, composed of petals; its pollen-producing stamens, and its ovule-bearing pistil. The pistil may be a single carpel (which has grown about the ovules and enclosed them); a number of separate carpels; or a group of carpels which have become fused together. In any case, the pollen necessarily is prevented from alighting directly upon the micropyle as it does in the gymnosperms, but instead is received upon a special projection of the pistil, the *stigma.* Here it germinates and sends down a pollen tube which ultimately reaches an ovule (Fig. 253).

The male gametophyte has practically disappeared (Fig. 254), for the nucleus of the microspore now divides only into the tube nucleus and the generative cell, and the latter produces two non-motile male gametes. The female gametophyte also is

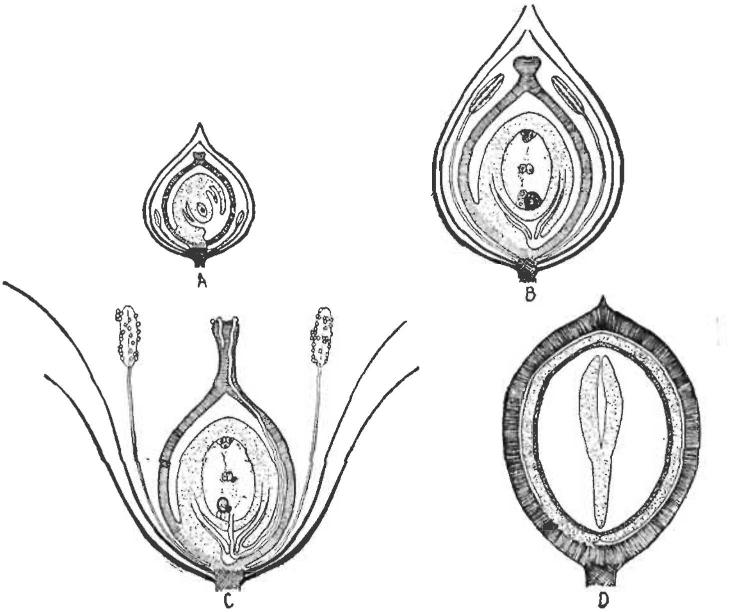


FIG. 253.—The process of seed production in a flowering plant. Longitudinal diagrams of flower and fruit. The calyx and corolla are solid black; the ovule, seed coats and embryo dotted; and the ovary wall, style, and stigma lined. *A*, young bud, the stamens and the single ovule beginning to develop. *B*, bud ready to unfold. The embryo sac within the ovule is fully developed and the egg (below) and the double endosperm nucleus (in the center) are ready for fertilization. *C*, fully opened flower. The anthers have burst and pollination has taken place, pollen grains being transferred to the stigma. Two grains have germinated, and the pollen tube from one of them has penetrated the style, entered the ovary, passed through the micropyle of the ovule, and discharged its contents—the two male gametes—into the embryo sac. Double fertilization is taking place, one male gamete uniting with the egg and the other with the endosperm nucleus. *D*, ripe fruit. Sepals, petals and stamens have dropped off; the ovary wall has hardened into the pericarp; the micropyle has closed; the integuments have become seed coats, and the ovule has now developed into the seed. The embryo, in the center of the seed, has grown from the fertilized egg, and the endosperm surrounding it (shown in white) from the endosperm nucleus.

greatly reduced (Figs. 255 and 256). The megaspore (the successful one of four originally produced in the nucellus) becomes much enlarged. Its nucleus divides into two, and one of these migrates to the end of the young embryo sac next the micropyle of the ovule and the other to the basal or antipodal

end. Here each nucleus undergoes two further divisions, so that at each end of the sac there now are four nuclei. One from each set then moves toward the middle and these two there fuse to form the *endosperm nucleus*. The three remaining at the micropylar end of the sac become definite cells, one of them the egg cell and the other two the *synergids*, probably the vestiges of an archegonium. The three antipodal cells represent all that

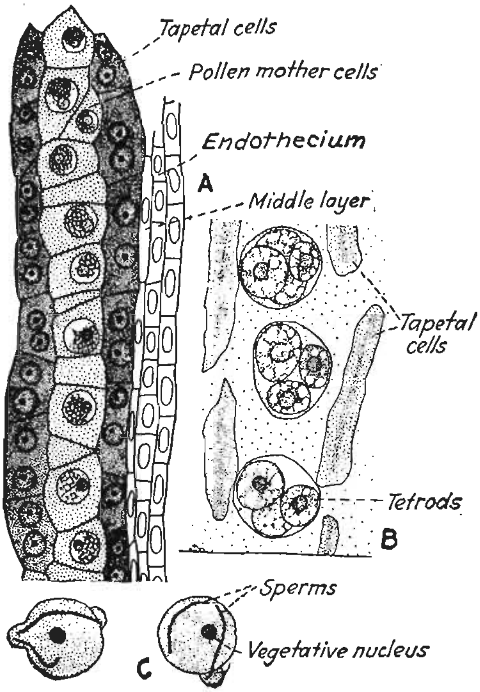


FIG. 254.—Development of the male gametophyte in an angiosperm (*Lactuca*). *A*, longitudinal section through young anther, showing pollen mother cell; *B*, microspores (pollen grains) in tetrads; *C*, mature pollen grains, showing the tube nucleus and the two male gametes in each. (*From Jones and Rosa.*)

remains of the abundant vegetative tissue of the sac as it is found in the gymnosperms. The gametophyte now consists of seven cells (or six cells and a naked nucleus) and is ready for fertilization. The two male cells pass down the pollen tube and enter the ovule. One fertilizes the egg nucleus, as usual, and from this union the embryo results. The other, however, instead of being eliminated, unites with the endosperm nucleus, and from the union of these two nuclei (the latter of which, it will be

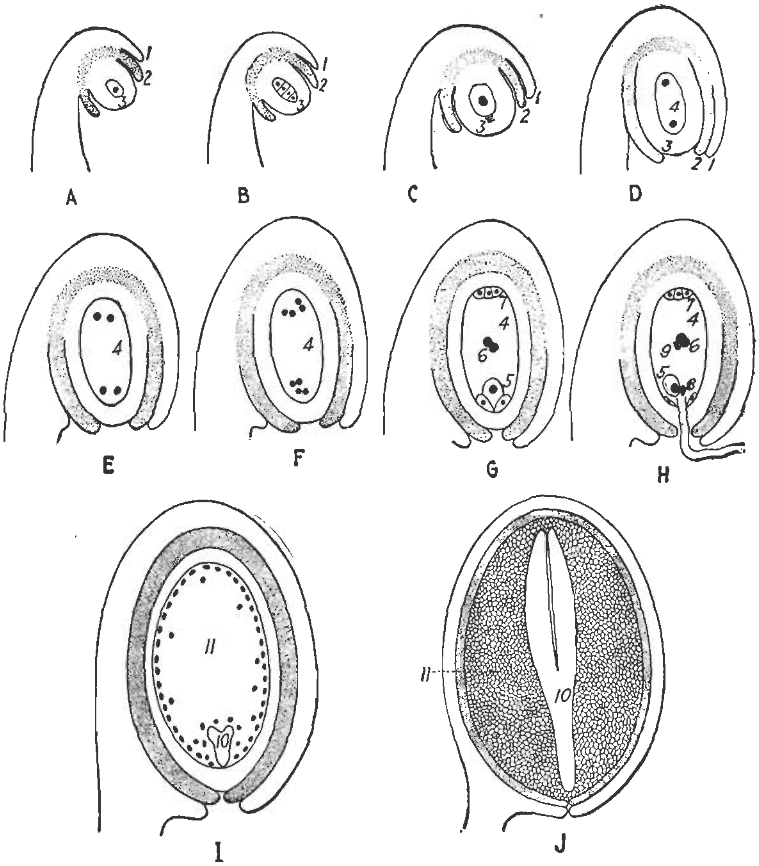


FIG. 255.—Development of the female gametophyte and seed in a dicotyledonous angiosperm. Longitudinal sections through the ovule and seed. *A*, very young ovule, the two integuments (1 and 2) beginning to appear and the megaspore mother cell evident within the nucellus (3). *B*, the megaspore mother cell has produced a row of four megaspores. *C*, three megaspores have aborted, the fourth is enlarging. *D*, the megaspore nucleus has divided into two, which now lie at opposite ends of the young embryo sac (4). *E*, each nucleus has again divided into two. *F*, each of the four nuclei has again divided into two, so that there are now two groups of four nuclei, one at each end of the embryo sac. *G*, one nucleus from each group has migrated to the center, and the two are uniting to form the endosperm nucleus (6). The three left at the end of the sac next the micropyle have formed the egg cell (5) and the two synergid cells. The three at the opposite end have formed the antipodal cells (7). The embryo sac is now fully developed and the egg is ready for fertilization. *H*, a pollen tube has entered the micropyle and discharged two male cells into the embryo sac. One of these (8) is uniting with the egg and the other (9) with the endosperm nucleus. *I*, the fertilized egg has grown into a small embryo (10) and the fertilized endosperm nucleus into a sac lined with nuclei (11). *J*, the mature seed. The integuments have hardened into seed coats, the micropyle is closed, the nucellus has disappeared, the endosperm sac has become a mass of solid endosperm, packed with food, and the embryo has reached its full size.

remembered, is already a product of fusion) develops the endosperm of the seed. The endosperm thus differs markedly in its

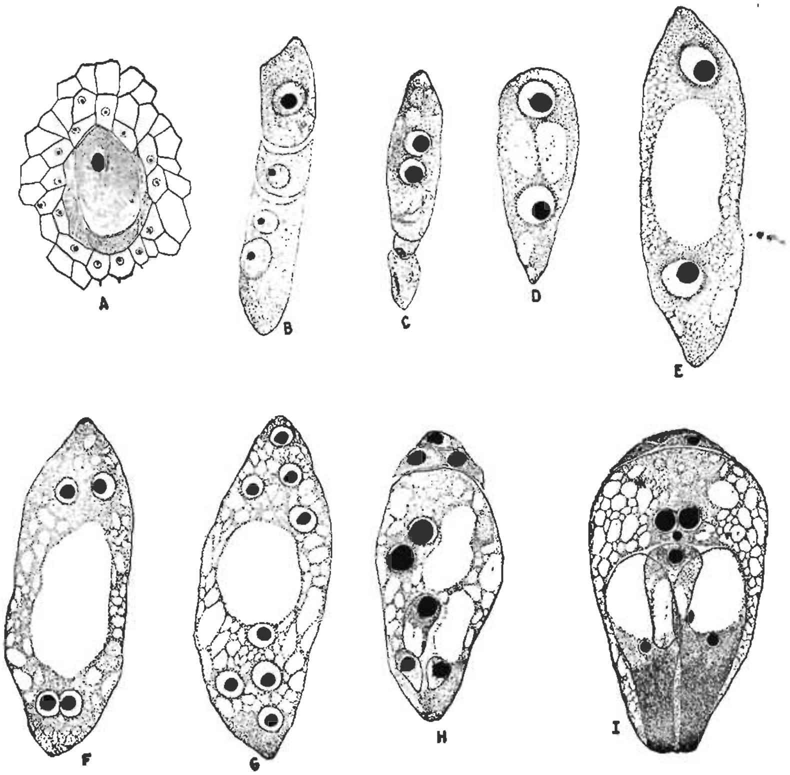


Fig. 256.—Development of the embryo sac, and fertilization, in the squash. *A*, megaspore mother cell, which is situated in the middle of a very young ovule. *B*, the four spores which develop from the mother cell. Three of these degenerate and disappear but the fourth, larger than the others, is the functional megaspore. *C*, the enlarged megaspore, in which the nucleus has now divided into two. *D*, a stage slightly later than *C*. The two nuclei have migrated to opposite ends of the young embryo sac. *E*, a still later stage, with the embryo sac much increased in size. *F*, each of the two nuclei has divided into two. *G*, each of these four nuclei has again divided into two, producing eight nuclei in all. *H*, the embryo sac, nearly mature. At the upper end (away from the micropyle of the ovule) are three antipodal cells. At the lower end (toward the micropyle) are the egg nucleus and the two synergids. The two endosperm nuclei in the middle have not yet fused. *I*, fertilization. One small male nucleus is about to unite with the endosperm nucleus (still double) and the other is about to fertilize the egg. (*From A. I. Weinstein.*)

history from that of gymnosperms. This phenomenon of *double fertilization* is a distinctive feature of reproduction in all

angiosperms. The development of the embryo and the ripening of the seed go on much as among the lower seed plants.

The angiosperms are divided into two clearly marked subdivisions, the dicotyledons and the monocotyledons.

Dicotyledoneae, or Dicotyledons.—As their name implies, these plants are characterized by the presence of two cotyledons

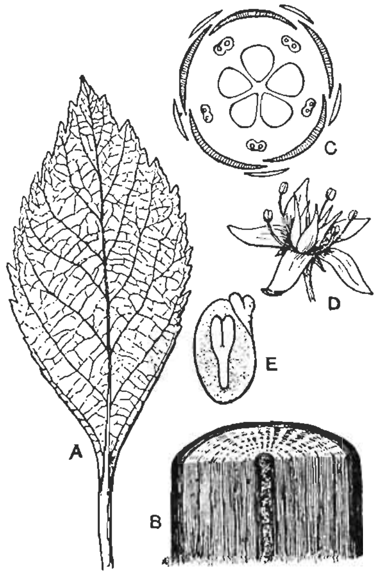


FIG. 257.

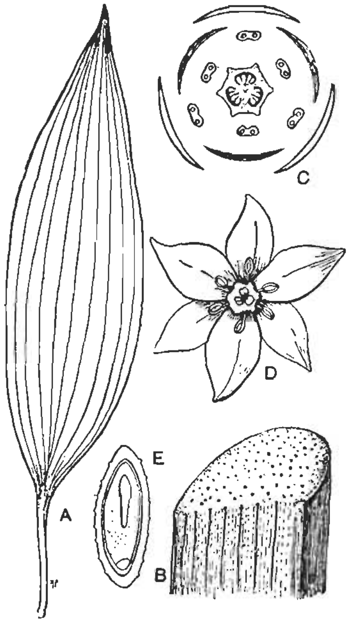


FIG. 258.

FIG. 257.—Characteristics of a typical dicotyledonous plant. *A*, leaf, netted-veined. *B*, stem, showing ring of wood and phloem. *C* and *D*, the flower, showing the floral parts in fives. *E*, section of seed, showing dicotyledonous embryo. (*From Gager's "Fundamentals of Botany," P. Blakiston's Son and Co., Philadelphia.*)

FIG. 258.—Characteristics of a typical monocotyledonous plant. *A*, leaf, parallel-veined. *B*, stem, showing fibro-vascular bundles irregularly scattered. *C* and *D*, the flower, showing the floral parts in multiples of three. *E*, section of seed, showing monocotyledonous embryo. (*From Gager's "Fundamentals of Botany," P. Blakiston's Son and Co., Philadelphia.*)

in the embryo of the seed, as opposed to the single one of monocotyledons, and they also display several other distinctive features (Figs. 257 and 258). These are: (1) the presence of netted venation in the leaf as opposed to the typically parallel-veined system of the monocotyledonous leaf; (2) the distribution

of the vascular system in a ring or tube separating an internal pith from an external cortex, as opposed to the irregularly scattered system of separate bundles in the monocotyledonous stem; and (3) the development of the floral parts ordinarily in multiples of four or five as opposed to the construction of the monocotyledonous flower, which is typically on the plan of three.

The dicotyledons, which include over 100,000 species, are generally divided into two main groups: the more primitive *Archichlamydeae*, in which the calyx and corolla are either very poorly developed, or have their various members entirely separate from one another; and the *Sympetalae*, in which the petals are typically united into a *gamopetalous* (or *monopetalous*) corolla.

Of the great array of groups which compose the dicotyledons only the most important will be mentioned. The Archichlamydeae include, among others, the following orders:

Amentiferae.—This group is now commonly divided into a number of subordinate orders, but in its larger sense it includes the oaks, beeches, chestnuts, hickories, walnuts, birches, alders, willows, poplars, and many others, all of them trees or shrubs. The perianth is scale-like or absent, the flowers dry and chaffy and arranged in a long, sometimes cone-like inflorescence, the *ament* or *catkin* (Fig. 122). They are prevailingly wind-pollinated. These plants were long regarded as the most ancient of the dicotyledons, but are now looked upon by many botanists as somewhat simplified and reduced forms.

Ranales (Fig. 259).—This great and varied group contains the buttercup, magnolia, laurel, and water-lily families and their allies, consisting of trees, shrubs, and herbs. Its flowers are pollinated by insects and are primitive in the sense that their parts, particularly the stamens and carpels, are typically numerous and have not become stereotyped in number and arrangement as is often the case among higher orders. The Ranales are regarded by many as the most ancient of the dicotyledons and as the center of origin for many of the higher groups.

Rosales (Fig. 260).—This huge order includes the saxifrage, rose, and legume families and their allies, comprising trees, shrubs, and herbs. The flowers are for the most part conspicuous and attractive, and furnish a large number of ornamental plants. Many important fruits and vegetables also find their place here. Regularity and symmetry characterize the flowers of the lower members but in the legume family (Leguminosae) the corolla

becomes markedly irregular, producing the butterfly-like or *papilionaceous* type.

Umbellales (Fig. 261).—This includes the dogwood family (mostly shrubs) and the carrot family (mostly herbs). The ovary in the group is inferior, the other floral parts being fused with it or borne upon it. The flowers are very small and arranged in compact, flat-topped compound umbels. This order marks the highest point of development among the Archichlamydeae.

FIG. 259.—One of the Ranales. Hepatica (*Hepatica triloba*), belonging to the Ranunculaceae.

FIG. 260.—One of the Rosales. Choke cherry (*Prunus virginiana*), belonging to the family Rosaceae.

The following orders are most important among the Sympetalae:

Ericales (Fig. 125).—These are the heaths, mountain laurels, blueberries, and their allies, most of them shrubby plants, and including many evergreens. The order is intermediate, in certain of its characters, between Archichlamydeae and Sympetalae.

Tubiflorales (Fig. 118).—Here are placed the morning-glory, phlox, borage, verbena, nightshade, mint, and figwort families, and a number of others, most of the members of which are herbs. The corollas are conspicuous and prevailingly tubular, and are regular in the lower families but extremely irregular in the higher

ones. The order comprises not only many garden flowers but a number of such important crop plants as the potato and tobacco.

Rubiales (Fig. 262).—Here are the madder and honeysuckle families, which are prevailingly trees and shrubs, although herbaceous species also occur among them. The flowers are most commonly on the plan of four and tend to be grouped in compact clusters.

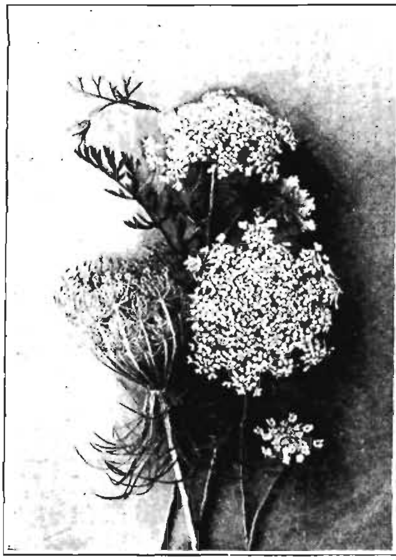


FIG. 261.—One of the Umbellales. Wild carrot (*Daucus carota*), belonging to the family Umbelliferae.

FIG. 262.—One of the Rubiales. Button-bush (*Cephalanthus occidentalis*), belonging to the family Rubieceae.

Campanulales (Fig. 266).—This order includes the gourd, bellwort, and composite families, most of the members of which are herbaceous. The last is the largest and most widespread family among angiosperms. Its flowers are arranged in complex heads, each of which somewhat resembles a single flower, the flowers at the margin of the head often being different from those in the center. The calyx is greatly reduced and becomes a scale-like *pappus* surmounting a single-seeded ovary. This family is a remarkably successful one and marks the highest point in evolutionary advance among the dicotyledons.

Monocotyledoneae, or Monocotyledons.—These plants, of which there are over 30,000 species, are characterized by the possession of a single cotyledon in the embryo, closed or parallel venation in the leaf, scattered vascular bundles in the stem, and a floral plan usually based on multiples of three. The group probably arose from somewhere among the primitive dicotyledons and its evolutionary advance has been more or less parallel with that of the latter group. With the exception of one order, monocotyledons are all herbs. Among the important orders are the following:

FIG. 263.—One of the Glumales. A sedge (*Carex*), belonging to the family Cyperaceae.

FIG. 264.—One of the Arales. The skunk cabbage (*Symplocarpus foetidus*), belonging to the family Araceae.

Glumales (Fig. 263).—These are the grasses and the sedges. The small flowers lack a typical calyx and corolla, are protected by chaffy bracts, and are arranged in clusters. They are wind-pollinated, except for those cases where pollination is affected directly, without external agency. As in the Amentiferae, their simple condition may have come about through reduction. The grass family includes the cereal grains, the most important of the crop plants.

Palmales (Fig. 265).—The palms are a tropical tree-like family in which the columnar trunk is surmounted by a cluster of large

leaves. The small flowers are borne in spikes and in some species are pollinated by wind and in others by insects. The perianth is very simple.

Arales (Fig. 264).—These are the aroids, a family of large herbs particularly abundant in the tropics and represented here only by the Jack-in-the-pulpit, skunk's cabbage, and a few other species. The leaves are typically large and, unlike those of most monocotyledons, are netted-veined. The very simple flowers,

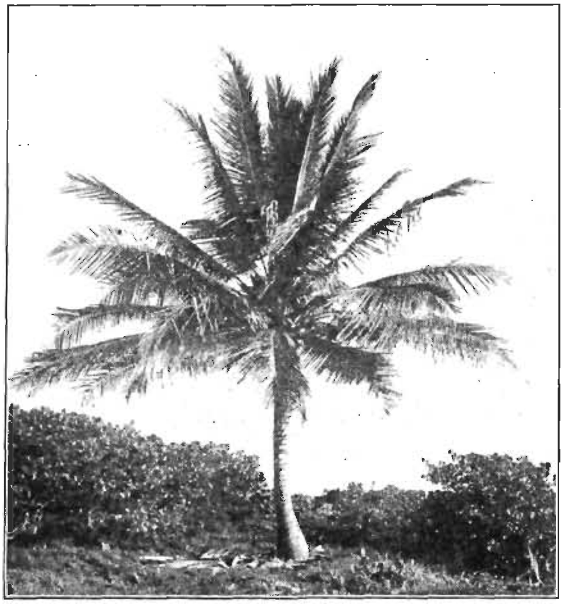


FIG. 265.—One of the Palmales. The coco-nut palm (*Cocos nucifera*). (*Courtesy of the New York Botanical Garden.*)

almost devoid of a perianth, are clustered on a fleshy *spadix* which is enveloped by a large and often brilliantly colored bract, the *spathe*.

Liliales (Fig. 113).—These include the lily, amaryllis, and iris families, perennial herbs with well developed bulbs or rootstocks. The species usually have a conspicuous perianth and provide some of the most beautiful of garden flowers.

Orchidales (Fig. 267).—The orchids are notable for the extreme irregularity and great beauty of their flowers, and their remarkable specializations for insect pollination. They are particularly

abundant and brilliant in the tropics, whence they have been introduced into the greenhouses of cooler climates as the most highly prized of exotics.

With the development of the composite and orchid families, the plant kingdom has reached the climax of its evolution.

Fig. 266.—One of the Campanulales. Yellow chamomile (*Anthemis tinctoria*), belonging to the family Compositae.

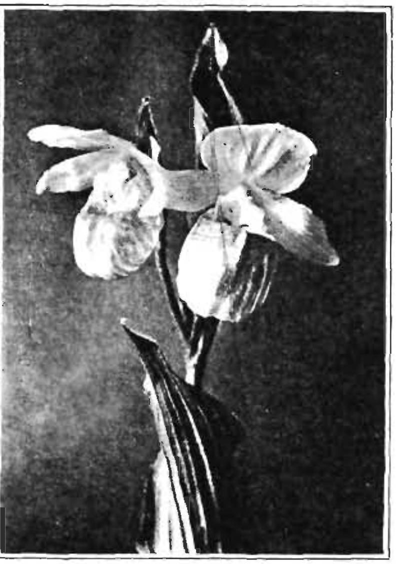


Fig. 267.—One of the Orchidales. Showy lady's slipper (*Cypripedium hirsutum*), belonging to the family Orchidaceae.

Plant Classification.—The main outlines of the classification of seed plants presented in this chapter and of the other divisions of the plant kingdom in the three previous ones is that generally accepted by most botanists, but with regard to many of its details there is still wide divergence of opinion. Ever since the dawn of botanical study, men have been endeavoring to construct an ideal system of plant classification and the results are very diverse. One of the earliest attempts used the resemblance in growth-habit as a basis and divided plants into three groups—trees, shrubs, and herbs. As botanists learned more about the vegetable kingdom, such crude systems were seen to be wholly inadequate, and resemblances of a much more deeply seated kind began to be noted, based on a larger number of characteristics. Thus the conception of plant *families* began to take form, and the

Rose family, the Carrot family, the Legume family, and many others were distinguished and described. There were still wide differences of opinion as to what the groups should be and how they should be subdivided, and there were almost as many "systems" as botanists. Indeed, on the theory which assumed that all plants had been created at the same time, it was difficult to

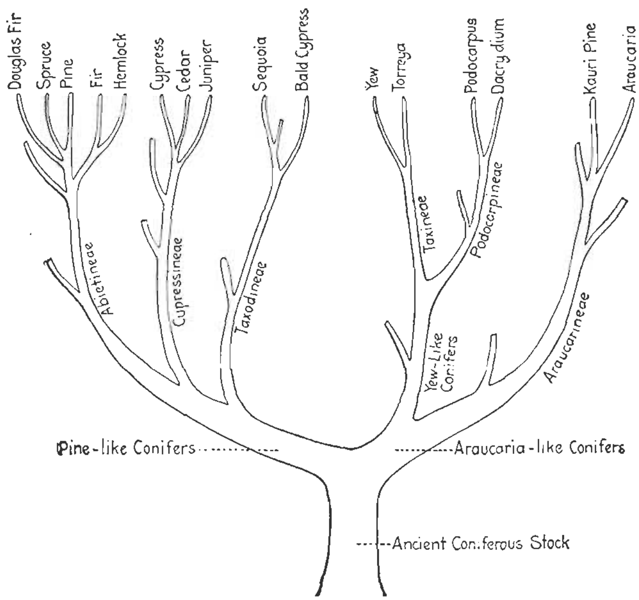


FIG. 268.—A suggested "family tree" for the Conifers. According to this hypothesis, the ancient coniferous stock long ago divided into two groups, each of which has given rise to three modern families or sub-families. Two of these (the Taxineae and Podocarpineae) are more closely related to each other than they are to the other families. Within the Abietineae there are evidently two distinct groups of genera. The branch stumps represent extinct groups. The twigs are genera of coniferous trees which are living today. Such a diagram as this makes it possible to show graphically the inter-relationships between the various members of a group of plants.

see why these well-marked groups of similar species should exist at all, and there really was no rational foundation for any system of classification.

The establishment of the theory of evolution in the latter part of the nineteenth century, however, threw a flood of light on the whole problem for it showed that resemblance among members of a plant group was not an arbitrary or chance one but was due to the fact that all the members *had descended from a common ancestor*. Classification became thereupon a definite effort to

work out a genealogy or "family tree" for the plant kingdom, or for a given group within it (Fig. 268), similar in its type to that which one might construct for any family. The problem confronting the taxonomist today, therefore, is not the recognition of certain rather vague "affinities" between plants, but simply the determination of what might be called their "blood relationships;" and during the past fifty years particular emphasis has been placed on the science of Phylogeny, which endeavors, through a study of fossil history, comparative anatomy, and other sources, to trace the complicated problem of ancestry and descent throughout the whole plant kingdom. The findings of this science are of great importance in providing a basis for classification. While there still are differences of opinion as to facts, everyone is agreed that the ideal to be attained is a system of classification which is truly a "natural" one, based on descent. As knowledge of the evolutionary history of the plant kingdom becomes more complete, systems of classification will grow more accurate and useful.

Groups within Groups.—Plant classification is far more complex, however, than a mere segregation of individuals into a series of distinct groups, for each group is further subdivided into smaller ones and each of these, in turn, into others still smaller. This system of "groups within groups" is familiar in methods of classifying all sorts of objects. An army, for example, has a definite system of organization or classification, whereby it is separated into a series of large groups, or divisions. Each division, in turn, is made up of brigades; each brigade, of regiments; each regiment, of battalions; each battalion, of companies; each company, of platoons; and each platoon, of squads. In this way every soldier occupies a definite and particular place in the organization. In the taxonomy of the plant kingdom a somewhat similar series of groups within groups has been recognized and its parts named, precisely as in a military organization. The most important of these groups are the *division*, *class*, *order*, *family*, *genus*, and *species*, although additional ones often are employed. Thus all the individuals which are like one another are grouped together and constitute a *species*, of which the dog rose may be taken as an example. This species is clearly very similar to a large number of other species,—the prairie rose, the swamp rose, the sweetbriar, and many others. All of these species, which have presumably descended from the same ancestor

originally, are grouped together as the rose *genus* (plural, *genera;* Fig. 269), the scientific name for which is *Rosa;* and each of the species also has a scientific name of its own, which for the dog rose is *canina.* From the general structure of their flowers, fruit, and other organs, it is believed that this rose genus is closely related to other somewhat similar genera, such as the cherries

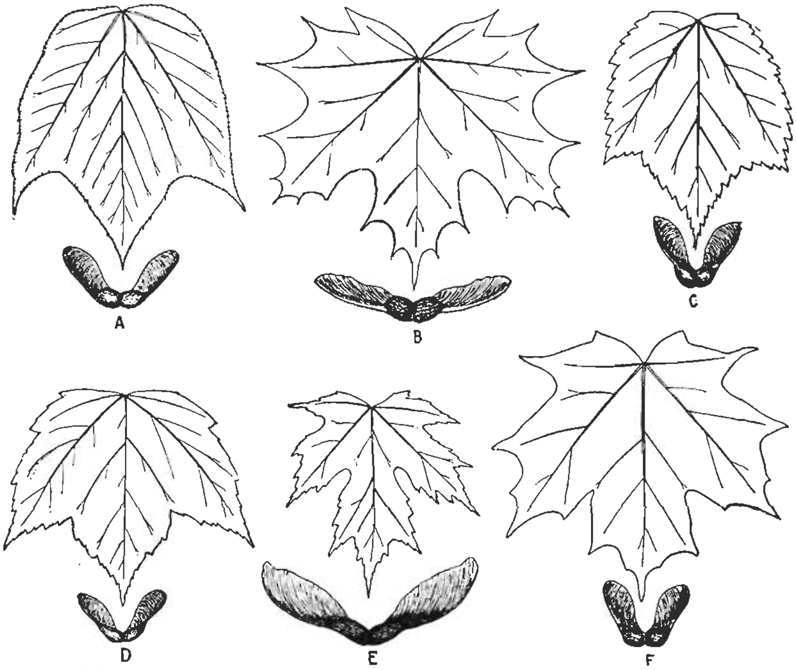


FIG. 269.—*Species* belonging to the same *genus.* Six species of maple (*Acer*) represented by leaf and fruit. Each species is readily distinguishable from the rest by its individual peculiarities, but in all the species the fundamental characteristics of the maple genus are evident. *A, Acer Pennsylvanicum; B, A. platanoides; C, A. spicatum; D, A. rubrum; E. A. saccharinum; F, A. saccharum.*

(*Prunus*), the apples (*Malus*), the hawthorns (*Crataegus*), the blackberries (*Rubus*), the strawberries (*Fragaria*), and others; and all of these genera are therefore grouped together into a still larger unit, the *family,* which in this case is the Rose family or *Rosaceae.* This is a large family, containing about 40 genera and 3000 species. It is evidently similar in many respects to certain other families, notably the Saxifrage family (Saxifragaceae) and the Legume family (Leguminosae). This group of families, which stand somewhat by themselves and probably are all related

to one another by descent, is called an order, in this case the *Rosales.** The Rosales are one of a large number of orders which constitute the great *class* of *Dicotyledoneae* or dicotyledonous plants. This is clearly distinguished from the other great class, the *Monocotyledoneae* or monocotyledonous plants; and these two classes comprise the subdivision *Angiospermae* or angiosperms. The angiosperms, together with the gymnosperms, make up the division known as the *Spermatophyta* or seed plants, one of the four main groups into which the plant kingdom is divided.

These units of classification include the most important ones, but large groups are often subdivided still further for purposes of convenience, so that one meets with the terms *variety, tribe, section, sub-family,* and others, each of which has its assigned place in the system. Every one of the thousands of groups in the plant kingdom has its own peculiar and distinctive characteristics by which it differs from every other group of similar grade, so that a botanist is able to place a newly discovered species in just the particular niche which it should occupy with reference to the plant kingdom as a whole.

Nomenclature.—The technical names for these various groups are derived from the Latin and Greek tongues, and although many plants have "common" names in the language of the country where they grow, the advantages of technical or "scientific" names are so great that they are used almost exclusively by botanists.

In earlier days, before the present system of naming plants had been introduced, the common way in which a botanist referred to a given species was to use a cumbrous descriptive phrase, usually consisting of several Latin nouns and adjectives. As different men often used different words, it frequently became a matter of doubt as to just what plant they were talking about, and much confusion resulted. It remained for the genius of the great Swedish naturalist Linnaeus to devise a method which should be simple and uniform. He invented the *binomial* system of nomenclature, so called because each species is given two names; first, the name of the genus of which it is a member, or its *generic* name, and following this a name applied distinctively to the particular species in question, or its *specific* name. The scientific name of the dog rose would thus be *Rosa canina.* This

* In general, the scientific name of a family has the ending *-ceae,* that of an order, *-ales.*

system is very much like that used in naming a person, where the "surname" is that of his family and the "given name" is distinctively his own. In plants, this order simply is reversed, the surname (generic name) coming first. The binomial system was first used extensively for plants in the "Species Plantarum," a great work published by Linnaeus in 1753, in which he described all plant species then known. This book is the foundation upon which the modern system of plant nomenclature is based.

In order to avoid confusion and to make perfectly clear what plant is meant, there is placed after the plant name the name (or its abbreviation) of the botanist who first used this name for the species in question. Thus the full name of the dog rose is *Rosa canina* L., which means that this particular name was conferred on the plant by Linnaeus. Disputes still arise as to just what certain species should be called, for different botanists have sometimes given different names to the same plant. Such questions must be settled by the adoption of universal rules and practices, and it is to be hoped that through them the nomenclature of plants may in time become perfectly uniform throughout the world.

Botanical Investigation.—One of the earliest tasks with which botanists were confronted was to name and classify the members of the plant kingdom, but even after the vast amount of work done by taxonomists, this task is yet far from completion. In the still more difficult problems of gaining a thorough understanding of plant structure and function, anything approaching final solution seems even more remote. An interest in the science of botany, both in its theoretical and its practical aspects, is steadily mounting and at no time in the past has as much active investigation been carried on in all fields of plant research as is being prosecuted today by governmental organizations, institutions of learning, and private agencies of all kinds. These studies are yielding abundantly and their published results are appearing in great numbers in books and in the form of papers in scientific journals. Indeed, it is becoming an increasingly difficult task merely to keep in touch with the advances in botanical knowledge. Marked progress is evident from year to year in the older fields of the science and new problems, of the utmost interest and significance, are continuously arising and pressing for solution. Botanical investigation has taken its place as one of the most important and fruitful fields of scientific work.

QUESTIONS FOR THOUGHT AND DISCUSSION

718. Why have plants which reproduce by seeds rather than those which reproduce by spores become the most successful part of the earth's vegetation?

719. Seed plants are relatively abundant as fresh-water species, but there are very few in the ocean. Explain.

720. Seed plants are sometimes called "Flowering Plants." Why is this not a very satisfactory name?

721. The archegonium is very much reduced in the gametophyte of seed plants. Explain.

722. With what structure in the ferns is (1) the embryo sac of seed plants comparable? (2) the pollen grain? (3) the ovule? (4) the nucellus?

723. Different terms are used for the various structures in the plant's life history among seed plants from those used among bryophytes and pteridophytes ("embryo sac" for female gametophyte, "anther" for microsporangium, and so on). What reason can you suggest for this difference?

724. What great groups of animals are there which obtain the bulk of their food directly or indirectly from other plant groups than the seed plants?

725. What various resemblances are there between cycads and ferns?

726. In what respect is the relation of the conifers to the rest of the gymnosperms similar to that of the ferns to the rest of the pteridophytes?

727. What relation can you suggest between the characteristic wood structure of conifers (as compared with that of angiosperms) and the tough and scale-like character of their leaves?

728. Staminate cones are much more numerous than ovulate cones on coniferous trees. Explain.

729. In regions where there are large coniferous forests, "sulphur showers" sometimes occur in the spring. What explanation can you suggest for these?

730. What advantages have angiosperms over gymnosperms which should have made them more successful and richer in species?

731. Is the endosperm of angiosperms gametophytic or sporophytic tissue? Explain.

732. If the gametophytic (or n) chromosome number of a given species is 12, how many chromosomes would you expect to find in the endosperm cells if the plant is a gymnosperm? if the plant is an angiosperm?

733. Give an example of a cultivated plant which is an annual herb; which is a biennial herb; which is a perennial herb; which is a shrub; which is a tree.

734. Which of these five plant types is of most importance in agriculture? Explain.

735. Why is there a larger proportion of herbaceous species in the flora of a temperate region than in the flora of a tropical one?

736. Angiosperms, and especially herbaceous angiosperms, have apparently evolved much faster and given rise to many more new species than have either pteridophytes or gymnosperms in a similar length of time. Explain.

737. What evidence can you suggest for the conclusion that dicotyledonous plants are more ancient than monocotyledonous ones?

738. What evidence can you suggest for the conclusion that families in which the flowers are irregular are more recent in evolutionary origin than families with regular flowers?

739. What evidence can you suggest for the conclusion that a flower with a large and indefinite number of floral parts, all free from one another, is more ancient in type than one in which the number of parts is smaller and more constant and where they are more or less united with one another?

740. In what respect may stamens and carpels be called "sexual organs"? In what respect is it incorrect to call them such?

741. What inference can be drawn as to the relative osmotic concentration of the cell sap in pollen grains and in cells of the stigma?

742. Why are the composite and orchid families regarded as constituting the highest points reached in the evolution of the plant kingdom?

743. What is the practical use of having a definite system of classifying plants into species, genera, families, and other groups?

744. What explanation have you for the fact that characters drawn from the flower rather than from the vegetative parts of the plant are chiefly used as a basis of classification in the seed plants?

745. Classify the following objects into a system of "groups within groups," stating briefly the characteristics by which each group may be distinguished from its coördinate groups, and making what is commonly known as a "key" to these objects: Apple, oak log, pumpkin, maple leaf, cotton fiber, apple blossom, potato, tulip bulb, peanut, turnip, pine cone, peach, spruce shingle, strawberry, automobile tire, squash seed, blade of grass, strip of birch bark.

746. In describing the plant kingdom in the latter chapters of this book much more space, relative to their number of species, has been given to some of the lower groups than has been accorded to the angiosperms. Why is this justifiable?

747. What advantages and what disadvantages has the scientific name of a plant as compared with its "common" or "popular" name?

REFERENCE PROBLEMS

216. What fossil evidence is there that seed plants evolved from fern-like ancestors rather than from plants resembling lycopods or horse-tails?

217. What are the two alternative theories as to the group of gymnosperms from which angiosperms have been evolved?

218. Seed plants are sometimes known as *Siphonogamia.* Why is this name appropriate for them?

219. The terms "Cryptogams" and "Phanerogams" are sometimes used to designate two main groups into which the plant kingdom may be divided, the former including thallophytes, bryophytes and pteridophytes, and the latter including seed plants. What objections are there to such a classification?

220. What family is most important as a producer of food plants, and what are some of the notable crop plants which belong to it? Name a few other families which have many important economic plants.

221. Name five cultivated plants which belong to the rose family; five which belong to the nightshade family; five which belong to the composite family.

222. What family is most important in the production of cultivated fruits?

223. What family is most important in the production of timber?

224. What species of wild-flowers are in particular danger of extermination in this region? What measures are being taken, or should be taken, to stop this?

225. Compare and contrast briefly the main features in the general systems of plant classification proposed by Engler and Prantl, and by Hutchinson.

226. Why is it that Latin and Greek are the languages from which the scientific names of plants and animals have chiefly been derived?

227. What is the scientific name of the American Elm? the Sugar Maple? the Apple? the Fringed Gentian? the Blue Flag? the Oat?

228. State the species, genus, family, order, and class to which each of the following plants belongs, and give the correct and complete scientific name of each: the White Pine; the Red Oak; the Potato; the Tiger Lily.

229. If two botanists each give a different name to the same plant species, what determines which name shall be accepted as the correct one?

230. Give the author and title of three important books dealing with the classification of seed plants, and outline briefly the content of each.

231. Name several botanical investigators who have done important work on the phylogeny and classification of seed plants, and state the notable contributions of each.

232. Give the derivation of the following terms, and explain in what way each is appropriate:

Antipodal (cells)	Nucellus	Species
Synergid	Genus	Papilionaceous

233. What is the nature of the work being done by the State Agricultural Experiment Stations?

234. Describe the organization and activity of the Bureau of Plant Industry in the United States Department of Agriculture.

235. Describe the organization and activity of the Botanical Society of America or any other important botanical society.

236. Name at least ten scientific journals devoted primarily to the publication of the results of botanical investigation.

237. Describe the purpose and organization of "Biological Abstracts," the chief botanical abstracting journal.

238. Give the citation for some recent scientific paper in botany, using the form found in Biological Abstracts, and then write a brief abstract of the paper.

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